THE ROLE OF MAMMALIAN HERBIVORES IN PRIMARY SUCCESSION OF THE TANANA RIVER FLOODPLAIN, INTERIOR ALASKA

by

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A

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ABSTRACT

I compared willow (*Salix*) communities along the Tanana River exposed to varying levels of herbivory to examine how herbivory influences the landscape distribution of vegetation. Moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) herbivory decreased plant biomass and canopy height and increased the proportion of dead stems in willow communities. Herbivory also shifted the age distribution of plants in willow communities towards younger age classes, and also decreased the number of communities dominated by willow on the landscape. A frame-based simulation model was built to incorporate the effects of herbivory and river fluvial dynamics on plant succession. My results show that herbivory, erosion and accretion are all necessary components to accurately model the landscape distribution of vegetation communities. Erosion/accretion had a major role in landscape vegetation patterns shifting the landscape toward earlier successional communities, while herbivory had a minor role, shifting the landscape towards later successional communities. The interactions among these biotic and abiotic processes account for the empirically observed landscape vegetation patterns.

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INTRODUCTION

This study focuses on riparian willow (*Salix spp.*) communities along a 250 km stretch of the Tanana River in Interior Alaska. My goal was to investigate both local and landscape effects of herbivory by moose (*Alces alces*) and snowshoe hares (*Lepus americanus*) on primary succession. The Tanana River system contains a rich diversity of animal life that relies on willow communities for food and cover. Whereas many factors are thought to be important in determining the distribution and abundance of willow stands, studying willow communities along a river system allowed me to eliminate several factors, such as seed dispersal and nutrient availability, from consideration. The accretion of river alluvium is the primary substrate for colonization first by willow, followed by alder (*Alnus tenuifolia*), poplar (*Populus balsamifera* L.), white spruce (*Picea glauca*) and black spruce (*Picea mariana*) stages (Walker et al. 1986).

Willows (*Salix spp.*) are the preferred winter food for many Alaskan herbivores, including moose and snowshoe hares, due to both their palatability and nutritional value (Bryant and Kuropat 1980). Willow abundance has been used by resource agencies to assess carrying capacity for moose and has been linked to the 10 year cycles of hare populations (Bryant et al. 1985). Thus, variation in willow abundance influences the abundance and distribution of many primary consumers and, as a consequence, secondary consumers, making willow an important species in floodplain ecosystems.

It is recognized that herbivores modify willow communities, both above and below ground, as well as effecting successional processes (Bryant et al. 1985, Bryant 1987, Pastor et al. 1988, Pastor and Naiman 1992, Moen et al. 1990, Kielland et al. 1997, Kielland and Bryant 1998). But whereas much is known about the small-scale effects of herbivores on willow communities, little work has been done to investigate the ramifications of herbivory at the landscape level. This is due in part to the complexities of investigating effects at a larger scale and the diversity of biotic and abiotic factors encountered.

Primary succession along the Tanana River generally follows the sequence described by Van Cleve et al. (1993): Following deposition of alluvium by the river, willow colonizes newly formed bars. Viable seeds of other species are usually present, but frequent flooding delays their establishment (Walker 1986). Terrace height increases as alluvium is repeatedly deposited by flooding events and eventually reaches a level at which species such as alder and poplar can persist. Typically after 5 years many species that represent later successional stages are present in these early successional sites (Walker et al. 1986). Early successional stands are dominated by willow and offer herbivores the highest forage biomass and forage quality of any successional stage, but provide the least cover. Peak production has been reported to occur in 15-20 year old stands (Wolff and Zasada 1979, Collins and Helm 1997, Weixelman et al. 1998). Alder replace willow as the dominant genera after 20 years. Alders form a closed canopy that is used by herbivores as cover, but is poor forage due to its high production of secondary compounds (Bryant and Kuropat 1980). The alder stage of succession lasts for approximately 25 -30 years and is eventually replaced as poplar overtops the alder canopy. While poplar stands provide cover and some forage for herbivores, much of the twig production is high in the canopy above the reach of most terrestrial herbivores with the exception of beaver (*Castor canadensis*). The poplar stage is eventually replaced by white and black spruce forests, which represent the end point of primary succession in riparian communities along the Tanana River.

I investigated the effects of biotic (herbivory) and abiotic (fluvial dynamics) factors on the establishment, longevity, and distribution of willow communities through field studies and modeling. I compared 2 areas exposed to high and low levels of herbivory to test hypotheses regarding the relative importance of these factors in 25 willow stands (13 in the high herbivory area and 12 in the low herbivory area). Results from the field study were incorporated into a model to investigate the impact of herbivory on landscape vegetation patterns and the effects of varying levels of erosion/accretion. I conclude that herbivory is a relatively minor factor influencing the longevity and abundance of willow

communities and influencing landscape vegetation patterns at low erosion and accretion levels, but has a large effect in combination with high levels of erosion and accretion. Thus, the interaction of biotic and abiotic processes exerts a major influence on vegetation patterns along the Tanana River.

Chapter 1

Effects of Mammalian Herbivory on Riparian Willow Communities along the Tanana River in Interior Alaska

ABSTRACT

I examined the effects of current moose and snowshoe hare herbivory on vegetation structure, demography and species composition of floodplain willow communities. Two study areas were initially selected based on differences in moose densities (0.2 per km^2 and 1.0 per km^2, Alaska Deptartment of Fish and Game 1998) and were comprised of *Salix alaxensis*, *S. brachycarpa*, *S. interior*, *S. lasiandra*, *S. novae-angliae*, *Alnus tenuifolia*, and *Populus balsamifera* L. I measured browsing intensity and plant architecture to verify differences in the present rates of herbivory. During the winter of 2001-2002, the combined browsing intensity of moose (*Alces alces*) and snowshoe hares (*Lepus americanus*) on forage species was 15% in the low density area and 69% in the high density area. Canopy height decreased from fall to spring in the high density area and remained constant in the low density area. Soil carbon and nitrogen were lower in the high density area. The densities of *S. alaxensis* and *S. novae-angliae* were lower in the high density area, while the densities of later successional species (*A. tenuifolia* and *P. balsamifera* L.) were greater. Differences were found in the proportion of dead:live ramets, indicating higher mortality in the high density area. Average and maximum ages of the primary forage species were younger in the high density area. River transects showed that high herbivory is associated with decreased numbers and sizes of willow communities on the landscape.

INTRODUCTION

Willow communities are established early in the successional sequence and dominate the open and closed shrub stages of primary succession on the Tanana River floodplain (Van Cleve 1993, Figure 1.1). Willow communities are an important resource for many vertebrates found along the Tanana River (Bryant and Kuropat 1980). This is especially

true for moose (*Alces alces*) that browse heavily on willow species (*Salix spp.*) during the winter months (Wolff and Zasada 1979, Collins and Helm 1997).

In 1989 exclosures were erected along the Tanana River to study the effects of moose and snowshoe hare (*Lepus americanus*) herbivory on succession as part of the Bonanza Creek Long Term Ecological Research (LTER) Program. This program documented the effect of herbivores on willow communities and has led many to consider the degree to which herbivores influence the distribution and abundance of willow communities. To date these studies have focused on decomposition, nutrient turnover, bellow-ground carbon allocation, and changes in the physical properties of the stand (Bryant et al. 1985, Kielland et al. 1997, Rossow et al. 1997, Kielland and Bryant 1998, Ruess et al. 1998). Apparent changes in successional turnover rates have been observed in the form of increased alder leaf fall in willow stands subject to herbivory (Kielland and Bryant 1998). Other studies have similarly concluded that herbivores can influence successional change (Wolff and Zasada 1979, Bryant and Chapin 1986, Walker et al. 1996, Binkley et al. 1997, Helm and Collins 1997). A possible explanation for these observations is that herbivores increased willow mortality and alder production.

For herbivores to change the rate of succession, a sufficient amount of browsing must occur. Willow responds to herbivory by growing fewer stems that are longer and less palatable (Bryant et al. 1985, Molvar et al. 1993). This constitutes a decrease in forage productivity in heavily browsed willow stands. As a result, more light penetrates willow canopies, increasing the productivity of later successional species. Subsequent shading by less palatable species decreases the production of secondary compounds in willow, again making them more susceptible to herbivory, and may accelerate successional turnover rates. As a result herbivory may lead to an earlier demise of the willow community and domination by late successional species.

Previous work at Bonanza Creek LTER has provided information on how moose and hares alter the local environment. This study expands these plot-level studies to the landscape level by observing differences in willow communities in a larger area subject to varying levels of browsing intensity. It concentrates on aboveground processes and expands these findings to a broader geographic range. I compared willow stands subjected to high and low levels of moose density to determine the impact of herbivores on plant architecture, density, age distribution, and landscape distribution.

HYPOTHESES

The general working hypothesis for this study is that browsing by herbivores influences plant longevity and successional turnover thereby exerting some measure of control over landscape vegetation patterns along the Tanana River. The proposed mechanism for how herbivores effect successional rates pertains to the removal of growth points by herbivores and the subsequent deposition of urine and feces that effect soil biogeochemistry (Kielland et al. 1997, Kielland and Bryant 1998). When leaves and twigs are removed, plants lose nutrient resources and some of their ability to photosynthesize. The effected plant must acquire resources and expend energy to replace lost structures. This removal also changes the architecture of the canopy (Bryant 1987, Kielland and Bryant 1998). As a result, more sunlight penetrates the willow canopy, benefiting understory plants, and reaches the soil, increasing soil temperatures. Higher temperatures increase microbial activity, which accelerates decomposition of plant and animal materials (Kielland et al. 1997). When combined with urine and fecal inputs, this increased nutrient turnover results in a greater availability of resources for plant uptake and growth. Other species, such as alder, benefit from the increase in available nutrient resources and sunlight, but unlike willow, alder incurs few negative effects of herbivory because vertebrate herbivores largely avoid this species (Bryant and Kuropat 1980). With higher growth rates and the shortening of the willow canopy, alder can dominate the canopy of a browsed willow community faster than it could if no browsing were present. When growing in the shade of an alder community, willows decrease their production of

secondary compounds, become more susceptible to herbivory, and are then removed from the community (Bryant 1987).

Hypothesis 1.1: *Increased herbivore density decreases the number of current annual growth stems on forage species by increasing the offtake by herbivores.*
This hypothesis is integral to this project because I must first determine that there are differences between the study areas and because it constitutes the first step of the proposed mechanism by which herbivores effect plant communities.

Hypothesis 1.2: *Increased herbivory levels decrease the height of the willow canopy.*
This hypothesis tests if the effect of herbivores in modifying the physical properties of the stand observed at the plot level are also evident in naturally occurring willow communities subjected to high herbivory levels. Herbivores have been observed to browse apical stems and as well as breaking the tops of shrubs. Decreasing the height of willow allows the non-forage species to dominate the canopy sooner and shifts the competitive balance toward later successional species.

Hypothesis 1.3: *High herbivory areas will have lower densities of forage species and a larger proportion of dead stems due to plant mortality caused by shortening the lifespan of the browsed species.*
While willow can tolerate some level of browsing by using stored nutrients to replace lost growth points with new buds, there is likely a limit to how much browsing a plant can sustain repeatedly. This, combined with shifts in competitive balance of the plant community induced by herbivory, is expected to result in changes in the species composition of the stand and an increase in the number of dead stems per unit area.

Hypothesis 1.4: *The shortened lifespan of willow caused by high levels of herbivory shortens the successional turnover time, changing willow communities into alder communities, and shifts the landscape toward later successional plant communities.*

I predict that the average age of forage species found in willow communities will be lower when exposed to increased herbivory levels due to plant mortalities and that the willow communities will have a shorter lifespan. The shorter duration of willow communities will be reflected on the landscape as a decreased abundance of willow communities in high herbivory areas.

OBJECTIVES

The objectives of this study were to:

1) estimate annual production and removal of stems, plant architecture, and the bite mass of forage species,
2) estimate canopy height, nutrient input, age distribution and species composition of willow communities, and
3) estimate the abundance and distribution of shrub communities.

STUDY AREA

The study was conducted along the Tanana River in Interior Alaska between Fairbanks (N 64° 50.50', W 147° 43.30') and Manley Hot Springs (N 65° 0.0', W 150° 36.0'). The Tanana River forms at the junction of the Chisana and Nabesna River and flows 380 km before entering the Yukon River at the village of Tanana (N 65° 10.4', W 152° 5.5'). Early successional floodplain soils are primarily sandy soils with a layer of silt loam on the surface. Willow typically colonizes new soils deposited along the river after 2 years and can persist for the next 20+ years (Van Cleve et al. 1993). Daily air temperatures in this region range from 28° C to –41° C in 2001 with an average daily temperature of -2° C. Annual precipitation in 2001 was 22 cm (National Oceanic and Atmospheric Administration 2003). Average snow depth recorded at the field sites in the spring of 2001 was 40 cm (S.E. = 1.7).

Because there are few estimates of hare densities in this region, two areas were selected based on winter moose density surveys conducted by the Alaska Department of Fish and

Game. Moose densities in the Fairbanks to Nenana area were estimated to be 0.4 moose/km^2 north of the Tanana River and 1 moose/km^2 south of the Tanana River, while the area around Manley, Alaska had relatively low densities, with estimates of 0.2 moose/km^2 (Alaska Department of Fish and Game 1998, Figure 1.2). The two areas are approximately 72 km apart and were chosen due to similarities in their topography as well as ease of access.

Area-wide moose densities have been estimated by the Alaska Department of Fish and Game several times during the last 10 years. Because moose densities at a specific location vary throughout the year, area-wide estimates represent the average potential moose use of the area. Moose densities have been relatively stable for the past 10 years (Alaska Department of Fish and Game 1998).

The snowshoe hare populations reached a peak in their 10 year cycle in 1999 (Bonanza Creek Long Term Ecological Research 2003). I assumed that the majority of the hare herbivory occurred during the period when the hare population was reaching its peak. Hare densities are assumed to be similar in the two study areas, varying slightly in the timing of peak and declines.

I compared 25 naturally occurring willow stands along the Tanana River between Fairbanks and Manley Hot Springs Slough (Appendix A, Table A1). Twelve of the willow stands were selected from the low density area near Manley Hot Springs. These stands were compared with 13 stands from the relatively high moose density area between Fairbanks and Nenana. Willow stands selected for this study were no more than 50 meters from banks of the Tanana River. Site selection favored mature felt leaf willow (*Salix alaxensis*) stands. These stands are composed of 5 *Salix* species *(S. alaxensis, S. brachycarpa, S. interior, S. lasiandra, and S. nova angliae), Alnus tenuifolia*, and *Populus balsamifera* L.

METHODS

Herbivore Use

The browsing intensities of moose and hares were measured on plants of each species closest to 3 randomly selected locations at each willow stand during the spring of 2001. I measured browsing intensity by counting the number of browsed stems and dividing by the total number of live stems. A maximum of 10 randomly selected current annual growth (CAG) twigs above the snow cover and below 3 m above the ground on each plant were included in the survey. Plant and twig selection continued until a total of 30 twigs per species had been recorded at each stand. Sampled twigs were classified as browsed by moose, browsed by hare, or unbrowsed. Browsed twigs were classified by herbivore based on the characteristics of the browsed point. Browse points that appeared jagged were classified as moose browsing, while points that were removed in a smooth cut were classified as hare browsing. While estimating browsing intensity, measurements were taken on the CAG base diameter and the diameter at the point of browsing (DPB, Kielland and Osborne 1998).

Forage species were also classified by their architecture to qualitatively measure historic browsing on plants in these areas. Plants were assigned to 1 of 3 categories: Unbrowsed, browsed, or broomed. Each category factors in current and historic browsing by looking at both live and dead twigs below 3 m above the ground for evidence of browsing, as well as looking at the growth form of the plant. Unbrowsed plants were defined as plants that display no evidence of moose or hare browsing. Browsed plants showed evidence of browsing on less than half of their twigs. Broomed plants had more than half of their twigs removed by browsing or exhibited stunted growth following the removal of the apical meristem.

The apical growth stem from 1 randomly selected plant of each species was harvested at each stand. The branch was divided into segments by cutting through the branch at each diameter that measured as a whole number in millimeters (i.e. 1 mm diameter, 2 mm

diameter, etc.). The twigs were then oven dried for 2 days at 50° C. The dry weights were then fit to a regression model based on the following equation to estimate off-take by herbivores and to estimate forage productivity

$$TwigBiomass = a + b * Diameter + c * Diameter^2$$

where a, b and c are estimated coefficients.

Canopy Height

Canopy height was measured in September 2001 (fall) and March 2002 (spring) to assess the effects of browsing on canopy height. At each stand, 50 locations were randomly selected during each sampling event. The height of the tallest plant regardless of species was measured to the nearest cm using a telescoping height pole.

Soil Chemistry

Five soil cores were collected at randomly selected locations from each of the 25 stands to determine the effect of herbivores on soil nutrient availability. After homogenizing the top 5 cm of each soil core (including both organic and inorganic layers), 20 g of soil were placed in a drying oven for 2 days at 60° C. The dry soil was then ground and passed through a 2mm sieve to remove coarse roots. After processing the samples 1g of soil was analyzed in a LECO 2000, CNS Analyzer to determine total C and N concentrations in the samples. Organic layer depth was measured on each soil core prior to homogenization and used as a covariate in analysis.

Feces

Moose and hare fecal samples were collected from each study stand during the winter. One pellet was collected from 5 randomly distributed plots from different pellet groups. The pellets were analyzed as a composite sample to observe differences in total N and C input to the soil in response to browsing pressure. Nutrient samples were oven dried for

2 days at 60° C and then ground in a 20 mesh Wiley mill. Once processed, 0.2 g were analyzed in a LECO 2000, CNS Analyzer for total C and N content.

Plant Density

Stem density was measured at 5 randomly selected 2 x 2 m plots at each stand in Spring 2001. Due to the high likelihood that an individual plant will produce multiple ramets originating below the soil surface, I defined an individual as a ramet that was at least 5 cm away from the nearest ramet of a plant of the same species. Dead ramets were considered unidentifiable and lumped into a single category to look at differences in overall plant survival in each of the browsing intensity areas.

Stand Age

The ages of willow stands were compared to determine how long the willow successional stage has persisted and how herbivory effects the age distribution of browse species. Twenty randomly selected plants of each species were harvested at each of the willow stands. After harvesting the plant, growth rings were counted under a dissecting microscope to determine plant age. The age of the oldest plant detected at each stand was assumed to represent the amount of time since the terrace was colonized and was used as a conservative estimate of the stand's age.

Community Abundance and Distribution

During the summer of 2002 a 21 km line transect was established along the river in each study area (2 transects total) to assess the average size and distribution of shrub communities. All shrub communities observed were classified by the predominant genera as willow (*S. spp.*) or alder (*A. tenuifolia)* communities. The location of each community was recorded using a Magellan 2000 Global Positioning System unit. Community size was estimated using a Bushnell Yardage Pro 600 Range Finder.

DATA ANALYSIS

Data were analyzed using SAS statistical software, SAS Institute Inc. 2001. All tests were evaluated at an α level of 0.05.

Herbivore Use

Herbivore use was assessed based on 3 estimates of removal (browsing intensity, plant architecture and forage availability and utilization) as well as changes in CAG base diameters and DPB. Browsing intensity percentages were arcsine transformed before analysis. ANOVAs were used to test for differences in the removal by moose and hares. Differences in plant architecture, CAG base diameters and browse selection between the high and low moose density areas were tested using nested ANOVAs, where measurements were nested in individual stands within the treatment areas. The analysis was repeated for all plant species.

Forage availability and utilization were calculated based on the twig diameter-biomass relationship in combination with species density, twig density per plant, CAG base diameters, and DPB measurements. A quadratic regression between twig diameter and biomass was calculated for each plant species and used to convert CAG base diameters and DPB measurements to available and removed twig biomass. The non-linear regression (Oldemeyer 1982) was preferred over the natural log transformed linear regression (Telfer 1969, Brown 1976) because it provided a normal scale standard error that could be used to calculate a standard error for forage availability and utilization using the delta method. Estimates of forage availability and utilization were compared using a t-test.

Area-wide moose densities and browsing intensity may not be correlated. For example I may observe areas with low herbivore densities and low forage availability resulting in high browsing intensity on a local willow community. Because complete vegetation survey was not feasible for this study, I was not able to determine the availability of

alternate food resources (non-riparian willow communities or other forage species) in study areas. However, habitat in this study area is patchy, which may result in discrepancies. I was initially forced to assume that there is a relationship between herbivore density and browsing pressure. I tested this assumption using an ANOVA to determine if there is a correlation between browsing intensity and area-wide moose densities.

Canopy Height

Overall differences in canopy heights between treatment areas were tested using a nested ANOVA that nested measurements from individual willow stands into the high or low moose density area. Differences in canopy height between the fall and following spring during a period when plants are typically dormant were analyzed within treatment areas using an ANOVA to determine if herbivory reduced canopy height.

Soil Nutrients

Differences in nitrogen and carbon between treatment areas were analyzed simultaneously using a multiple analysis of covariance test. Organic layer depth was used as a covariate in this analysis to account for differences in soil nutrient content resulting from variation in leaf litter accumulation. Soil nutrient data were analyzed using the natural-log transform to meet assumptions of normality. Differences in fecal input between the high and low moose density areas were analyzed using an ANOVA.

Plant Density

Differences in the species composition of willow communities between the high and low moose density areas were analyzed using ANCOVAs with stand age as a covariate for species density. Stand age was defined as the oldest plant age detected in a willow stand.

Plant Mortality

The percent of dead and live plants was analyzed using nested ANOVAs after arcsine-square root transformation. The nested ANOVAs tested for differences between the high and low moose density areas while accounting for differences between willow stands.

Age Distribution

The mean ages of each plant species in the two areas were compared using nested ANOVAs. Changes in average minimum stand age (maximum plant age detected) were evaluated using an ANOVA.

Community Abundance and Distribution

A single transect along the river corridor the length of each study area was used to assess the number of willow and alder communities present. This precluded the calculation of means and standard errors and therefore statistical testing. However, an ANOVA was used to test for differences in the size of willow and alder communities between areas.

RESULTS

Herbivore Use

Overall, herbivores browsed more twigs in the high moose density area ($F_{1, 16} = 35.85$, $P < 0.001$). This difference was attributed to moose ($F_{1, 19} = 21.81$, $P < 0.001$), since snowshoe hare browsing did not differ significantly between areas ($F_{1, 19} = 2.58$, $P = 0.124$). At the species level, only the percent of *S. alaxensis* and *S. novae angliae* twigs browsed by moose were significantly different between areas ($F_{1, 19} = 24.26$, $P < 0.001$ and $F_{1, 12} = 13.34$, $P = 0.003$, respectively). No differences were found in forage selection by snowshoe hares (Figure 1.3). I did not observe any browsing by moose or snowshoe hares on *S. novae-angliae* and *P. balsamifera* L. in the low density area.

Of the forage plants in willow communities in the high density area, 3% were unbrowsed, 11% were browsed, and 86% were broomed. In the low density area, 0% were

unbrowsed, 32% were browsed, and 68% were broomed (Figure 1.4). The difference in the proportion of forage plants assigned to the browsed architectural category was significant ($F_{1, 24} = 4.49$, $P = 0.044$). *S. alaxensis* was the only individual species with significant differences in the browsed (7% in the high density area and 35% in the low density area) and broomed (93% in the high density area and 65% in the low density area) architectural categories, suggesting high historical use of this species by herbivores in the high density area. No other species differed significantly between areas.

CAG base diameters did not differ between the two areas with the exception of *S. lasiandra* ($F_{1, 12} = 8.06$, $P = 0.015$). Similarly, DPB differences were not significant in any forage species. The greatest differences were observed in *S. lasiandra* with average DPB of 4.0 mm and 2.3 mm in the high and low density areas respectively ($F_{1, 12} = 4.05$, $P = 0.068$).No differences were found in twig biomass at a given diameter between areas.

Combining information on plant densities, twig densities, twig base diameters, and twig biomass for forage species, it was determined that 657 kg/ha (S.E. = 95.1) of CAG biomass were available to herbivores in the high density area and 750 kg/ha (S.E. = 125.0) in the low density area. Herbivores removed 220 kg/ha (S.E. = 26.7) in the high density area and 42 kg /ha (S.E. = 7.8) in the low density area during the winter (Table 1.1). Utilization of CAG was 33.5% and 5.6% respectively.

Canopy Height

Overall canopy height was higher in the low density area ($F_{1, 23} = 7.25$, $P = 0.013$). Mean canopy height in the high density area decreased from 233 cm in the fall to 211 cm in the spring ($F_{1, 19} = 9.43$, $P = 0.013$), while it did not change in the low density area where it maintained an average height of 282 cm between seasons ($F_{1, 11} = 0.04$, $P = 0.845$).

Nutrients

Total carbon and nitrogen in the soil were highest in the low density area and were positively correlated with organic layer depth ($r = 0.778$, $n = 60$, $P < 0.001$ and $r = 0.807$, $n = 60$, $P < 0.001$, respectively) and stand age ($r = 0.801$, $n = 60$, $P < 0.001$ and $r = 0.834$, $n = 60$, $P < 0.001$ respectively), which were greater in the low density area. Soil nutrients in the high density area were also correlated with organic layer depth ($r = 0.685$, $n = 65$, $P < 0.001$ and $r = 0.663$, $n = 65$, $P < 0.001$ for carbon and nitrogen respectively), but were poorly correlated with stand age ($r = 0.21$, $n = 65$, $P = 0.093$ and $r = 0.253$, $n = 65$, $P = 0.042$ for carbon and nitrogen respectively). No differences between areas were associated with herbivory levels ($F_{1, 24} = 0.15$, $P = 0.294$ and $F_{1, 24} = 0.94$, $P = 0.341$ for carbon and nitrogen respectively). Similarly, the C to N ratio did not differ between areas. Soil nitrogen concentrations were directly correlated with soil carbon levels ($R^2 = 0.95$, Figure 1.5).

Fecal samples obtained during the winter showed significant differences between browsing species in carbon concentration (0.49g C / g feces from hare compared to 0.51g C / g feces from moose), but the differences were biologically negligible. Fecal nitrogen concentration did not differ between areas or species (Mean = 0.01 g N /g feces, S.E. = 0.034; $F_{1, 21} = 0.05$, $P = 0.819$; and $F_{1, 21} = 0.53$, $P = 0.477$ respectively). However, there was a greater density of moose pellet groups in the high density area than in the low density area (mean = 0.24 and 0.03 pellet groups / m^2 respectively, $F_{1, 23} = 12.17$, $P = 0.002$), while the density of hare pellet groups did not differ between areas (Mean = 0.2 pellet groups / m^2, $F_{1, 23} = 0.01$, $P = 0.905$). This results in the estimated addition of 29.6 g C / m^2 and 0.6 g N / m^2 to soils in the high density area and 4.8 g C / m^2 and 0.1 g N / m^2 to soils in the low density area through fecal deposition.

Plant Density

Willow communities were dominated in both areas by *S. alaxensis* with all other species making up less than 30% of the community (Figure 1.6). No differences between the

high and low moose density areas were found in the density of willow or of later successional species. However, differences were found in the density of standing dead ramets ($F_{1, 23} = 40.19$, $P < 0.001$) as well as the relative proportions of live to dead plants (Figure 1.7), suggesting high plant mortality in the high moose density area.

Age Distribution

The mean age of plants in the willow communities was significantly younger in the high density area ($F_{1, 25} = 8.77$, $P = 0.007$, Table 1.3). Figure 1.8 shows the age distribution of each species, with significant shifts in the means of *S. alaxensis, S. lasiandra,* and *S. nova-angliae* ($F_{1, 23} = 9.44$, $P = 0.005$; $F_{1, 20} = 4.62$, $P = 0.044$; and $F_{1, 20} = 4.75$, and $P = 0.042$ respectively). The lack of differences between the age distributions of *A. tenuifolia* may indicate a delay in colonization by this species in the low density area. The earliest colonization in the low density area is estimated to have occurred when stands were 13.6 years (S.E. = 1.02) on average, while colonization ages of stands in the high density area were estimated to be 9.7 years (S.E. = 0.83) on average ($F_{1, 18} = 8.99$, $P = 0.008$). Colonization time of *P. balsamifera* L. did not differ between the low and high density areas (Mean = 7.8 years, S.E. = 2.53 and Mean = 6.6 years, S.E. = 1.46 respectively), but this species occurred on only 4 out of 12 willow communities in the low density area as opposed to 12 out of 13 communities in the high density area, suggesting a difference in colonization between the two areas.

No difference between areas was detected in the average community age. However, several of the willow communities in the low density area were older than any willow community in the high density area (Figure 1.9). Natural variation in the minimum age of selected stands precludes statistical testing of community age. Since all of the mature willow communities found in both study areas were aged, I conclude that the lack of older stands in the high density area is evidence of differences in the successional transition of willow to alder communities between these two areas.

Community Abundance and Distribution

Willow communities comprised a larger percentage of the shrub communities in the low density area than in the high density area (Table 1.4, Figure 1.7). The size of willow communities along the Tanana River tended to be larger in the low density area (9.2 ha) in contrast with the high density area (4.0 ha, $F_{1, 52} = 1.16$, $P = 0.287$), however, a size comparison of known age communities showed stands to be significantly smaller in the high density area when age was used as a covariate ($F_{1, 22} = 13.88$, $P = 0.001$).

Alder communities were equally abundant in both areas, but stand size was smaller in the low density area (mean = 7.9 ha) than in the high density area (mean = 3.2 ha, $F_{1, 42} = 5.62$ $P = 0.022$). Alder communities were therefore a smaller percentage of the river corridor in the high density area (See Appendix A, Table A2 for the locations of shrub communities).

DISCUSSION

The changes observed in plot level studies conducted by the Bonaza Creek Long Term Ecological Research Program (Bryant et al. 1985, Kielland et al. 1997, Kielland and Bryant 1998) along the Tanana River (were also observed at the landscape level. Herbivores modified physical properties of willow communities as well as altering the number and sizes of communities on the landscape. These changes linked browsing by moose and hares to a shortening of the longevity of individual willow plants and willow communities as a whole.

As is typical of landscape studies, the design of this project involves a form of pseudoreplication since there was no distribution of treatment levels in a random pattern. As such the findings of this study are specific to the area studied.

The effects of herbivory documented in this study were attributed to moose and snowshoe hares. While beaver (*Castor canadensis*) has also been identified as an

herbivore that can modify habitat and effect succession (Moen et al. 1990, Naiman et al. 1994, Nolet 1994, Helm and Collins 1997), I documented some beaver activity in only 2 of the 25 stands. Beaver were not considered an important factor in this study. Similarly, I observed little defoliation by insects during the two years of my study, but I can make no inferences about its importance historically.

Browsing intensity in the study areas was positively correlated with moose density. Browsing intensity differed between areas for moose on the community level and for individual plant species. Snowshoe hare browsing intensity differed between areas when all plant species were pooled, but no differences were found between areas for individual plant species. Similarly, no differences were found in hare fecal densities. The differences observed are however attributed to herbivory by moose and hares because it is the combined effects of browsing by these two herbivores that effected ecosystem processes in the study areas. The primary forage species for moose in riparian areas along the Tanana River was *S. alaxensis* followed by *S. lasiandra* and *S. nova-angliae* while hares browsed primarily on *S. alexensis* and *P. balsamifera* L.

Herbivores utilized 5 times more of the available CAG in the high than the low density areas. Offtake by herbivores altered canopy height, nutrient input, plant densities, plant survival, and the abundance and distribution of willow communities. Forage architecture and canopy height both showed evidence of historic and current heavy browsing of the dominant plant species, *S. alaxensis*, in the high moose density area, while the low density area showed evidence of light historic and current levels of browsing. This difference allowed me to make a comparison of the effect of browsing on willow communities. This comparison clearly shows that herbivores have a significant effect on the physical properties of the stand.

No differences were found in DPB or in CAG basal diameter between the two areas (Appendix B) that were predicted by optimal foraging theory (Kielland and Osborne

1998) and by documented plant response to herbivory (Bryant 1987) due to high standard errors associated with these estimates. Variation in bite-size diameter may have been caused by the patchy nature of willow communities along the Tanana River, which may have lead to variation in nutritional stress experienced by individual herbivores and resulted in high variation in bite sizes. Alternate food sources in non-riparian areas were not examined in this study, but likely constitute a portion of the diet of herbivores, particularly in the summer (LeResche 1973).

Fecal carbon input was approximately equal to the annual carbon input from leaf litter fall (Kielland et al. 1997). Soil carbon concentrations at the landscape level were similar to those observed at the Bonanza Creek LTER exclosures, where soil carbon concentrations were higher inside herbivore exclosures than in areas with herbivores. Decreased soil carbon concentrations in stands exposed to herbivory resulted from increased nutrient turnover and decreased fine root production (Kielland et al. 1997). Failure to detect differences in the amount of soil nutrients in willow communities exposed to different levels of herbivory may be attributable to variability in stand age, increased organic layer thickness in the low density stands and differences in the frequency of flooding events that leach nutrients from the soil. The increase in organic layer in the low density area was attributed to prolonged exposure to leaf litter fall and root production resulting from the older age of willow communities as compared with the high density area.

High herbivory levels increased the proportion of dead ramets. This finding implies that high herbivory levels increased willow mortality. However no differences were found in the density of species in willow communities. This lack of differences may be due to vegetative reproductioin of the willow plants replacing dead ramets or due to site selection. Since mature willow stands were selected, all of the stands had high willow densities and low densities of later successional species.

The absence of *S. brachycarpa* and the infrequent occurrence of *S. nova-angliae* in the low moose density area may be a consequence of taller canopy height which may select against shorter, small-leaved plants. I do not think that seed dispersal would limit the distribution of these species along the Tanana River since the light seeds of *S. brachycarpa* and *S. nova-angliae* can be dispersed long distances by wind.

Shifts in the age distribution of the three primary forage species and the increase in the density of standing dead ramets implies a decreased lifespan in plants that can be attributed to herbivory. The subsequent increases in density of later successional species imply an accelerated successional turnover from the willow to alder successional stage due to moose and hare browsing. This conclusion was further supported by my observations on the river transects that show not only a change in landscape composition, but also a change in the size of shrub communities. These change result in a landscape with fewer, smaller willow communities and larger alder communities associated with increased herbivory.

I conclude that herbivores modify the local environments and influence successional processes and species composition at the landscape level. These changes shift the landscape towards later successional stages by increasing the transition rate from willow to alder. This information strengthens the argument that herbivores set the stage for later successional plant species to dominate the canopy. This study contributes to our understanding of the factors controlling willow abundance and distribution as well as the physical and chemical characteristics of the community when subjected to different levels of herbivory. Many investigators have observed an increased association of terrestrial vertebrates with riparian willow communities as one moves north across Alaska. Factors controlling willow distribution and abundance are therefore expected to result in changes in the distribution and abundance of other organisms.

Management Implications

Wildlife managers have known that the carrying capacity of a range may be altered by climatic conditions such as precipitation and temperature. This study indicates a feedback between the herbivore and its environment that may accelerate the decline in habitat and subsequently the carrying capacity of the range through an increase in successional turnover rates from early to later successional stages. This shift should be considered when deciding if a range can support increased population sizes, particularly when the population is thought to be nearing the habitat's carrying capacity. If natural processes do not rejuvenate the habitat fast enough to sustain wildlife populations, wildlife managers could initiate prescribed burns to provide resources for herbivore populations or attempt to decrease the number of herbivores through hunting. The findings from this study provide insight to the effects of browsing pressure on successional turnover rates and the need for proactive management steps to prevent a decline in animal populations.

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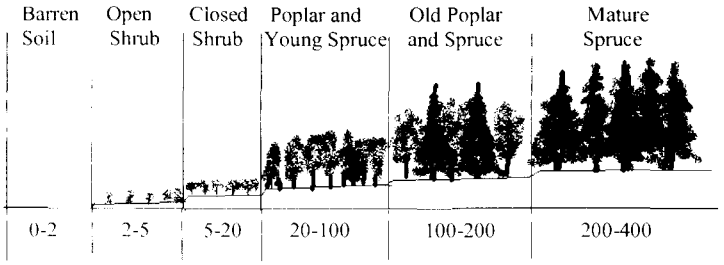


Figure 1.1. Successional sequence along the Tanana River floodplain in Interior Alaska (modified from Van Cleve et al. 1993).

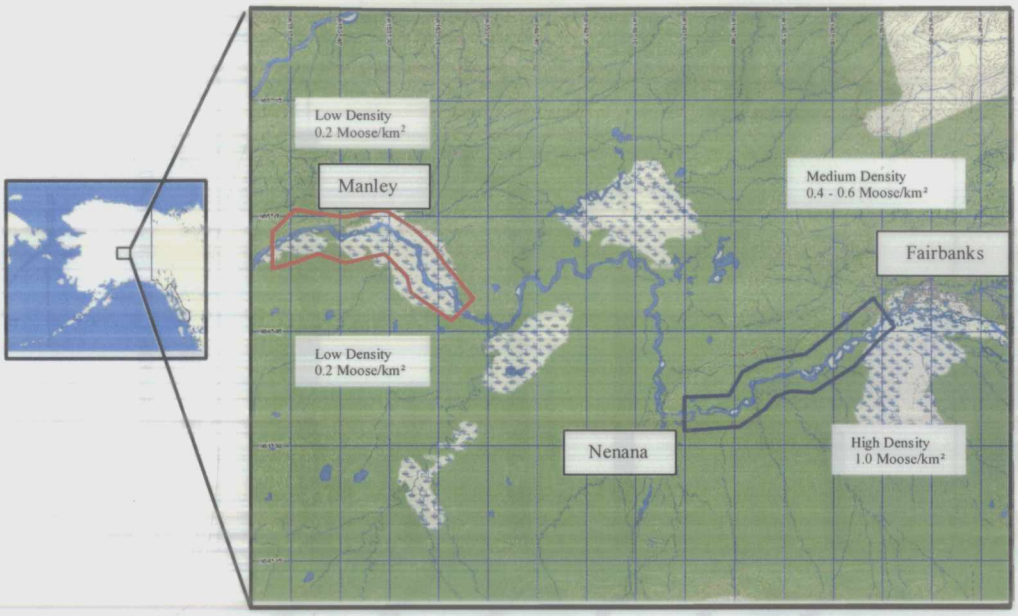
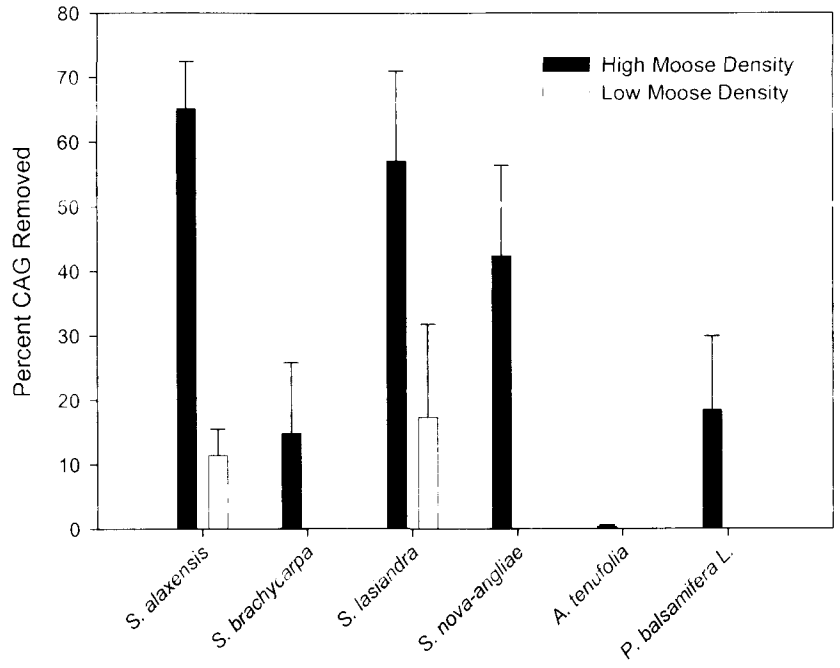


Figure 1.2. Tanana River study area showing the distribution of moose densities in relation to Fairbanks and the two treatment areas. The red boundary indicates the low moose density study area, and the blue boundary indicates the high moose density study area.

a)



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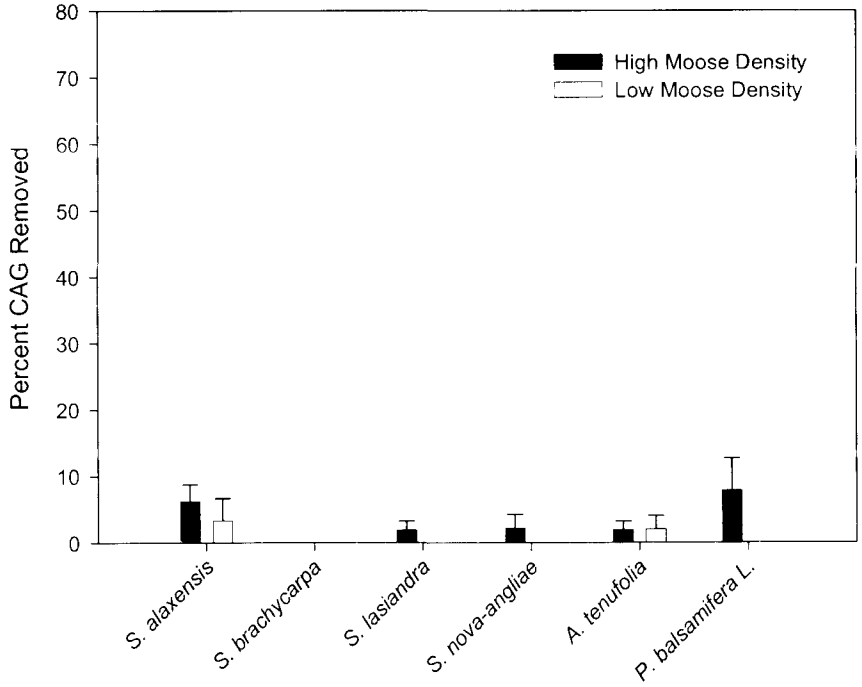

Figure 1.3. Browse removal by moose (a) and snowshoe hares (b). Bars indicate means and S.E.'s are shown above the bars.

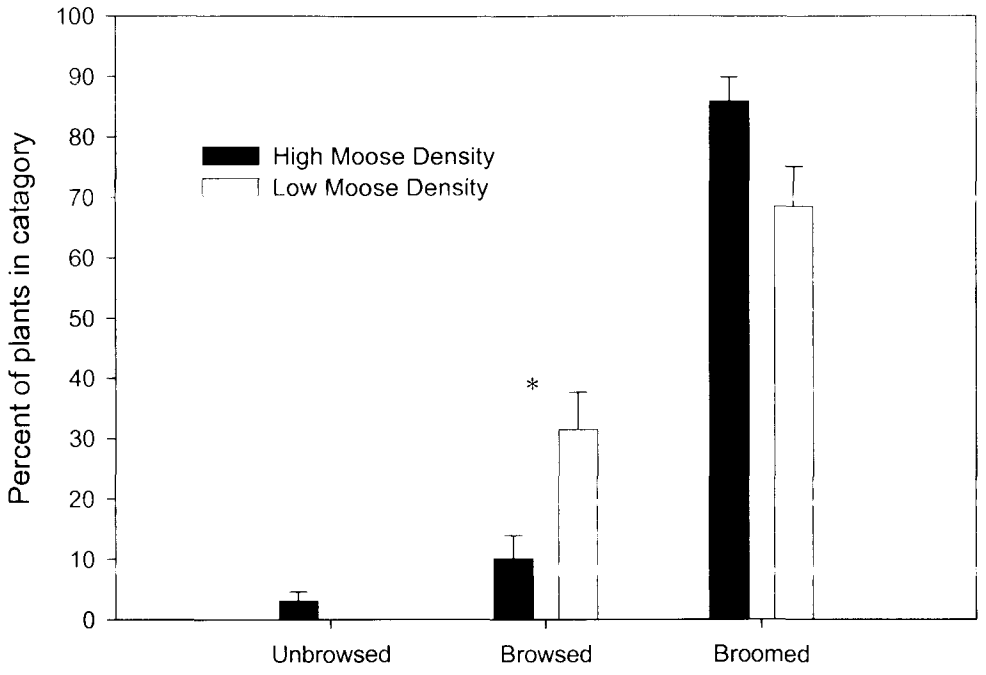

Figure 1.4. Architecture of forage plants in willow communities along the Tanana River. Bars indicate means and S.E.'s are shown above the bars. Significant differences are indicated by *.

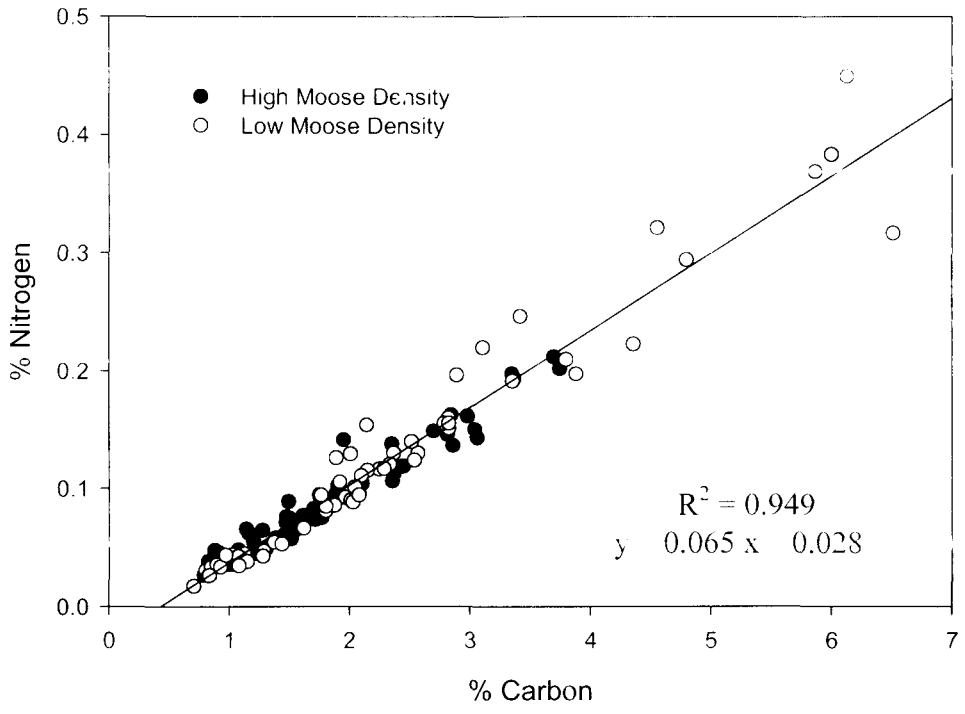

Figure 1.5. Relationship between soil carbon and nitrogen content in willow communities along the Tanana River.

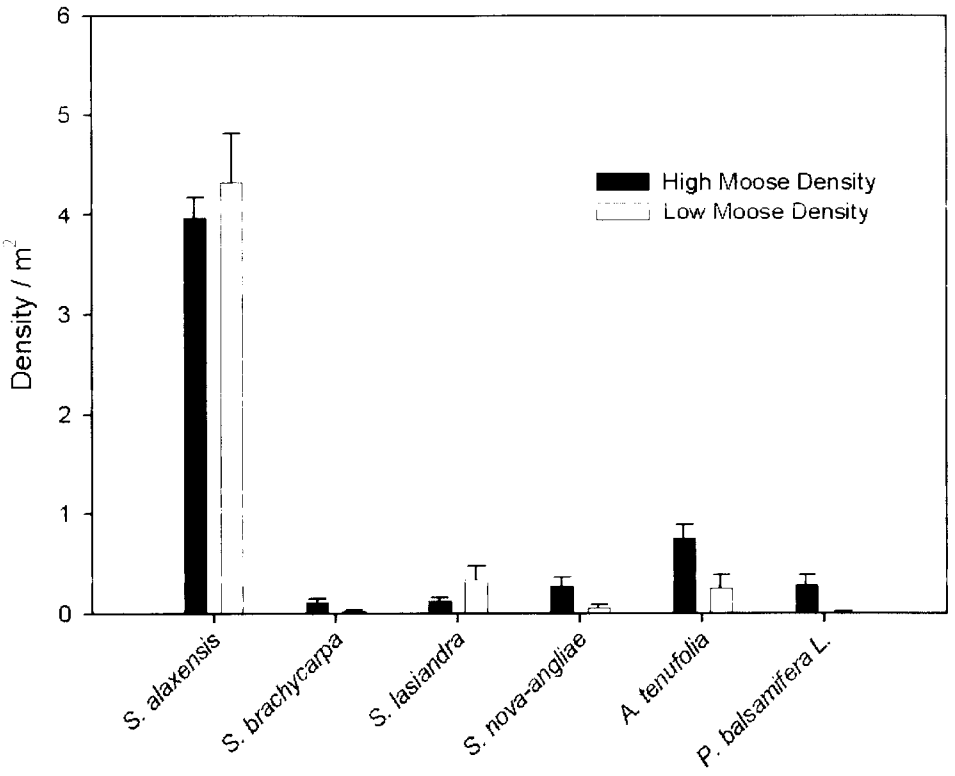

Figure 1.6. Species composition of willow communities on the Tanana River. Bars indicate means and S.E.'s are shown above the bars.

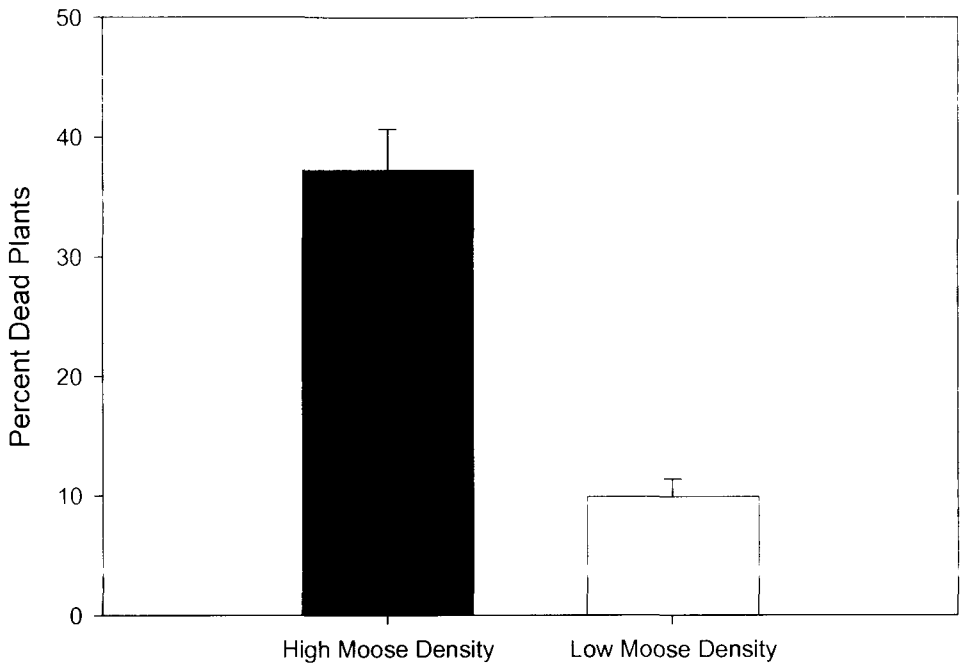

Figure 1.7. Proportion of dead plants in willow communities along the Tanana River in the high and low moose density areas. Bars indicate means and S.E.'s are shown above the bars.

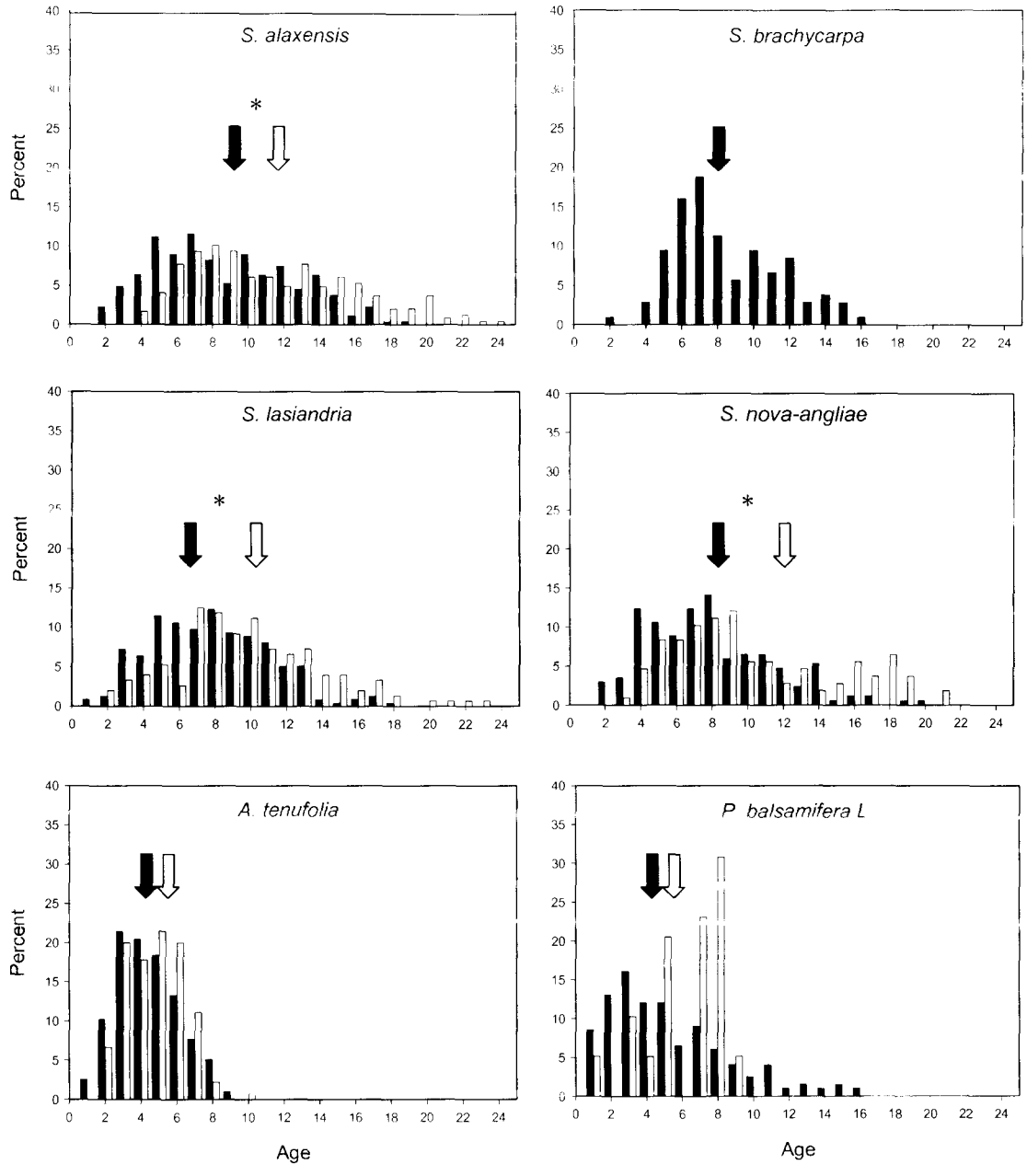

Figure 1.8. Age distribution of 4 willow species, alder and poplar in willow communities found along the Tanana River in the high (solid) and low (open) moose density areas. Arrows indicate the average age. Significant differences are indicated by *'s.

Figure 1.9. Age of the 25 willow communities used as field sites in the high and low moose density areas along the Tanana River.

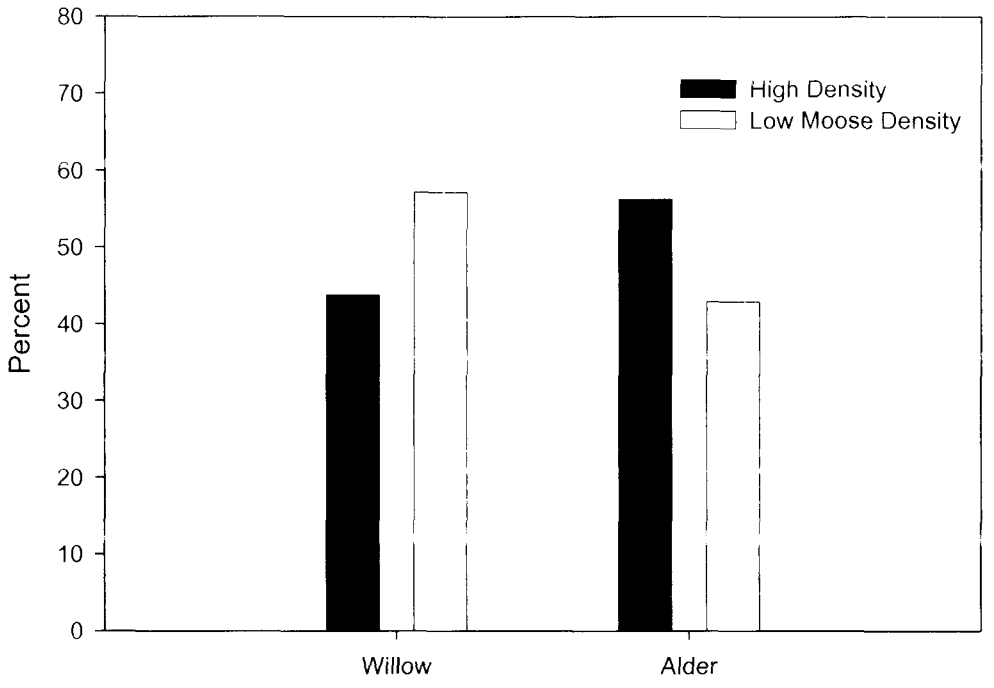

Figure 1.10. Proportion of shrub communities classified as willow or alder on a 21km transect along the Tanana River in each study area.

Table 1. Twig Off-take (kg/ha) by herbivores in willow communities along the Tanana River in the high and low moose density areas. Mean (S.E.)

	S. alaxensis	*S. brachycarpa*	*S. lasiandra*	*S. nova-angliae*	*P. balsamifera*	Total	Moose and Hares
Moose							
High Moose Density	158.6 (17.6)	0.7 (1.2)	7.52 (2.1)	2.1 (0.9)	1.3 (0.6)	170.5 (22.4)	219.5 (26.7)
Low Moose Density	30.4 (4.9)	0.0 (0.0)	1.0 (0.6)	0.0 (0.0)	0.0 (0.0)	31.4 (5.5)	42.4 (7.6)
Hare							
High Moose Density	47.1 (3.56)	0.0 (0.0)	0.1 (0.3)	0.9 (0.4)	1.7 (0.6)	48.9 (4.3)	
Low Moose Density	11.0 (2.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	11.0 (2.28	

Table 1.2. Density (stems/m^2) comparison of plant species found in willow communities along the Tanana River in the high and low moose density areas.

	High Moose Density		Low Moose Density		
	Mean	S.E.	Mean	S.E.	P-value
S. alaxensis	4.0	0.2	4.3	0.3	0.345
S. brachycarpa	0.1	0.03	0.0	0.04	0.073
S. lasiandra	0.1	0.1	0.3	0.1	0.021
S. nova-angliae	0.3	0.1	0.1	0.1	0.055
A. tenuifolia	0.8	0.1	0.2	0.1	0.004
P. balsamifera L.	0.3	0.1	0.0	0.1	0.005
Standing Dead Ramets	2.7	0.1	0.6	0.1	<0.001

Table 1.3. Comparison of mean and maximum ages (yrs) of species found in willow communities along the Tanana River in the high and low moose density areas.

	High Moose Density		Low Moose Density		
	Mean Age (S.E.)	Max	Mean Age (S.E.)	Max	P-Value
A. tenuifolia	4.4 (0.1)	9	4.7 (0.1)	10	0.106
P. balsamifera L.	5.3 (0.3)	16	6.1 (0.4)	9	0.162
S. alaxensis	8.6 (0.2)	19	11.8 (0.3)	37	<0.001
S. brachycarpa	8.5 (0.3)	16	N/A	N/A	N/A
S. lasiandra	7.9 (0.2)	18	9.8 (0.3)	23	<0.001
S. nova-angliae	7.9 (0.3)	20	10.4 (0.5)	21	<0.001

Table 1.4. Comparison of the proportion of shrub communities dominated by willow and alder along a 21 km transect performed along the Tanana River in each study area.

	High Moose Density	Low Moose Density
River Distance (km)	20.9	20.9
Straight Line Distance (km)	16.4	18.0
Observed Stands	32	42
# of Willow Communities	14 (43.8%)	24 (57.1%)
# of Alder Communities	18 (56.2%)	18 (42.9%)
Total Willow Area (hectares)	47.0 (45%)	274.2 (66%)
Total Alder Area (hectares)	58.5 (55%)	142.9 (34%)

Chapter 2

Modeling the influence of herbivory and fluvial dynamics on landscape vegetation patterns in floodplain communities on the Tanana River, Alaska

ABSTRACT

A frame-based simulation model was designed to examine the interaction of herbivory and fluvial dynamics on landscape vegetation patterns. The model was validated by comparing the simulated landscape to naturally occurring variation in erosion/accretion and herbivory levels along the Tanana River. Increases in herbivory decreased the proportion of early succession pixels and increased the proportion of late succession pixels in the simulated landscape. Erosion and accretion worked as antagonists to herbivory, increasing the amount of early successional pixels and decreasing later successional pixels. Low herbivory combined with high erosion/accretion had the greatest effect on the ratio of willow to alder and produced the highest forage availability on the landscape. These findings support the hypothesis that herbivory, erosion, and accretion are important factors influencing successional dynamics on the Tanana River floodplain and underscore the importance of biotic and abiotic interactions in shaping landscape vegetation patterns.

INTRODUCTION

Rivers are dynamic systems that deposit new mineral soils as channels shift or dry up. Willow species (*Salix spp.)* colonize these newly formed, unoccupied soils due to their fast growth and large seed production (Walker et al. 1986). Once established, willows dominate the open shrub stage of succession and are soon replaced by alder (*Alnus tenuifolia*) during the closed shrub stage. Over time shrub communities are replaced by later successional species such as balsam poplar (*Populus balsamifera*) and white spruce (*Picea glauca*) (Van Cleve et al. 1993).

Several studies have examined the influence of herbivores on willow communities and found changes in the physical and chemical properties of the stands (Bryant 1987, Kielland et al. 1997, Kielland and Bryant 1998). Herbivores have also been linked to changes in the longevity of willow communities, influencing the rate of successional turnover (Walker et al. 1986, Bryant 1987). These findings indicate that herbivory can influence early successional communities and may have consequences for vegetation patterns at the landscape level (Magoun and Dean 2000).

Erosion of soil can remove plant communities from all stages of succession and may lead to the accretion of bare soil on which primary succession can begin anew. Fire can also reverse the successional sequence to earlier states depending on its intensity. Fire is particularly important in older stands dominated by spruces (*Picea glauca* and *Picea mariana*) (Wolff and Zasada 1979, Van Cleve et al. 1983, Helm and Collins 1997, Weixelman et al. 1998), which typically have a high fuel load. However there is no consensus as to whether fire is an important factor in early successional floodplain communities (Magoun and Dean 2000).

This study examined changes in vegetation communities on a simulated landscape to evaluate the relative effects of herbivory, erosion and accretion along the Tanana River in the Interior of Alaska. It incorporated data from previous process studies at the plot level and expanded these findings to the landscape level. I developed a spatially explicit model to determine if the effect of herbivory in the willow stage of succession can alter landscape vegetation patterns. The simulation progresses through the successional sequence and allows the landscape to be effected by fluvial processes. The model incorporates the effect of herbivory by moose (*Alces alces*) and snowshoe hares (*Lepus americanus*) on willow communities, to determine if the differences I documented (Chapter 1) have ramifications on the landscape level. This modeling exercise supports the hypothesis that herbivory is an important factor in determining landscape vegetation patterns, shifting the landscape towards later successional stages.

HYPOTHESES

The general hypothesis of this study is that the combined effects of herbivory, erosion, and accretion alter landscape vegetation patterns by changing the transition time between successional stages. Herbivory primarily alters the duration of the willow stage by increasing plant mortality and by altering the competitive balance between species in the stand. Erosion and accretion alter successional patterns by removing late successional communities and initiating primary succession. In support of this hypothesis I propose the following:

Hypothesis 2.1: *High herbivory levels increase the proportion of late successional stage communities on the simulated landscape by decreasing the duration of the willow stage.* I predicted that the shorter duration of willow stage caused by high herbivory levels will decrease the proportion of willow communities on the landscape. In the model, the tree stage represents all late successional stages dominated by trees (from the poplar stage to the black spruce stage). Because the tree stage in this model serves as an end point for succession in riparian areas and the model incorporates a fixed area, decreasing the amount of willow communities in the simulated landscape increases the amount of late successional communities.

Hypothesis 2.2: *High erosion/accretion levels decrease the extent of late successional communities on the simulated landscape by removing late successional stands and by initiating primary succession.*

Acting as an antagonist to herbivory, erosion reduces the amount of late succession communities by removing a higher proportion of the soils occupied by these stages. Accretion of river alluvium initiates primary succession and thereby increases the proportions of shrubs on the landscape.

Hypothesis 2.3: *The effect of low herbivory coupled with the effects of high erosion/accretion interact to produce a simulated landscape with a high proportion of shrub communities.*

I predicted that the greatest interaction between abiotic and biotic factors would occur when erosion and accretion levels are high. The converse is not true since abiotic factors are needed to produce willow communities in which herbivores exert their greatest influence. Because herbivory acts as an antagonist to abiotic effects, the combination of low herbivory and high erosion/accretion levels should increase the proportion of shrub communities.

Hypothesis 2.4. *At high herbivory levels, herbivores influence the quantity of available forage by decreasing the above ground biomass (AGB) of forage plants and by decreasing the proportion of willow communities on the simulated landscape.*

I incorporated the effects of herbivory on willow AGB per m^2 that were observed at field stands into the simulation model to observe changes in the amount of available forage. I predicted that the local effects of high herbivory levels combined with the decreased duration of the willow stage at high herbivory levels would decrease the total amount of available forage in the simulated landscape and that the amount of available forage will be further reduced by the decrease in the total proportion of willow communities.

OBJECTIVES

The objectives of this study were to:

1) determine how herbivory can influence landscape vegetation patterns
2) evaluate the effect of herbivory on future willow biomass available to herbivores, and
3) determine if there is an interaction between biotic and abiotic factors effecting vegetation communities.

STUDY AREA

This model simulates biotic and abiotic processes along the Tanana River in Interior Alaska. The active floodplain of the Tanana River ranges from 300 m to 2000 m wide (Collins 2001) and extends 824 km through boreal forest communities (Ott 2001) exposed to a wide range of herbivory levels. Primary succession along the Tanana River was described by Van Cleve et al. (1993), who reported a transition from bare soil to a willow stage followed by an alder dominated stage, a poplar dominated stage and culminating white and black spruce forests.

The simulated landscape is 1 x 2 km with a 60 m wide river running through it. The landscape is divided into 10 x 10 m pixels representing 100 m^2 areas. All pixels that are not classified as river begin as bare soil with the potential to be colonized by plant species according to the successional sequence described by Van Cleve et al. (1993, Figure 1.1).

METHODS

Model Overview

The model simulates the combined effects of herbivory and erosion/accretion on successional patterns in the active floodplain along the Tanana River. The model is based on the ALFRESCO model developed by Rupp et al. (2000). ALFRESCO is a spatially explicit model that simulates transient landscape dynamics, including vegetation succession and fire. The simulation model described in this paper simulates a landscape that transitions through the successional sequence from river to bare soil, and ultimately to the tree stage (Figure 2.1). The rules for successional change are dictated by changes in species density for most successional stages and by changes in the biomass ratio of poplar and alder to willow during the willow stage. Each model variation was run for 250 years and was replicated 100 times. The model duration of 250 years was set a priori using coefficient of variation analysis on model outputs to determine when landscape parameters had stabilized.

The model assumes that colonization of the soil is not an obstacle to community establishment because seeds are easily distributed from nearby communities by the river and wind (Wolf and Zasada 1986), that erosion equals accretion in every year of the model, and that succession always follows the order described by Van Cleve et al. (1993, figure 1.1).

The model does not allow for reversion to earlier successional states (e.g., reversion of spruce forest to shrubs following a fire). This is not expected to occur often, due to low fire periodicity in riparian areas along the Tanana River. Most disturbances along the active floodplain are caused by erosion and revert the landscape back to primary succession (i.e., bare soil). Early successional stages may also be skipped altogether (e.g., occasionally bare soil is colonized by poplar and skips the shrub stages entirely) which is a possibility not addressed by this model. It should also be noted that the model frames represent the dominant species only. Previous frame species are not necessarily eliminated, and may remain in the next frame.

Succession

There are five successional frames in the model. Each frame represents a successional stage, and the transition between frames occurs in a set order. Because transition to a new stage of succession is determined by the colonization and growth of the new plant community, each frame monitors the development of plants that will define the next successional stage with the exception of the river frame (Appendix C).

The river frame spans the simulated landscape as a cosine wave that moves through the model at rates that correspond to erosion/accretion rates along the Tanana River (Ott et al. 2001). The simulated river has a fixed width of 60 m. While this is less then the average total width of the Tanana River's active floodplain as a whole, it is used to represent an active channel along this braided river. As the river moves across the

landscape it "erodes" pixels of any other frame type and leaves bare soil pixels in its wake.

The bare soil frame is colonized by willow according to trends observed at field sites along the Tanana River. Once the willows reach the critical density within a pixel, the pixel transitions into the willow frame. The transition from the willow to alder frame is based on the ratio of willow above ground biomass (AGB) to alder and poplar AGB, which will be referred to as the AGB ratio. Kielland and Bryant (1998) reported this biomass ratio to be a good indicator of the successional status of a willow stand. Willow AGB was modeled using a logarithmic equation using data observed in willow stands along the Tanana River. Similarly, alder and poplar AGB were modeled with data obtained along the Tanana River, but the growth equation is an exponential curve reflecting their continued growth after the transition to the alder frame.

Density of poplar was used in the model as an indicator of the status of a pixel as it changes from the alder frame type to the frame dominated by trees. Initial and critical transition densities reflect those reported by Van Cleve et al. (1993). The tree frame of this model represents stands dominated by poplar and spruce. The model allows for this category of successional stages to revert to bare soil through erosion/accretion, but does not consider fire even though fire becomes a more important factor, particularly in older spruce stands.

Herbivory

I compared willow communities effected by high (69% of current annual growth browsed) and low levels (15% of current annual growth browsed) of herbivory to obtain estimates of the effect of herbivory on biomass and density in stands of various ages. The differences were summarized in one herbivory variable reflecting the proportion of available twigs browsed, which can be altered in the model to simulate the effect of varying levels of herbivory on the model's vegetation. A similar comparison was

performed on later successional species (alder and poplar) found in willow communities that are used in the AGB ratio for the transition from willow to the alder frame.

The effect of herbivory on willow biomass was derived from field studies along the Tanana River (Chapter 1). Naturally occurring biomass reflects the willow mortality and growth under browsed conditions. Because of this link between herbivory and willow biomass, herbivory on non-willow species is excluded from the calculation of herbivory levels at the field sites for this application. The main willow species utilized along the Tanana River and used to assess herbivory pressure were *S. alaxensis*, *S. nova-angliae* and *S. lasiandra*. These species account for 84% of the individual plants in willow communities along the Tanana River, and are the most heavily browsed, while the remaining forage species, *P. balsamifera* L. and *S. brachycarpa*, account for 5 % of willow communities (Figure 1.6).

I modeled the 100% herbivory scenario in the model testing phase, and it predicted that willow AGB remains at 1 g /m^2 throughout the time a pixel is classified as in the willow frame, which is what I would expect if herbivores removed 100% of the Current Annual Growth. This scenario assumes that moose and snowshoe hares remove every growing point and every subsequent growing point the willow produces following colonization. This scenario is not known to occur naturally, since herbivores have been shown to prefer taller willow plants for food (Collins and Helm 1997, Kielland and Osborne 1998) and cover (Franzmann and Schwartz 1997, Courtois et al. 1998, and Weixelman et al. 1998). Furthermore, short willow plants are usually covered during the winter by snow and are unavailable to herbivores during the period of time when moose focus on willow twigs as a primary source of food. As a result, the 100% herbivory models were excluded from data analysis.

Erosion/accretion

The abiotic factor of interest in this study is the rate at which soils are eroded and deposited along the river system. Erosion and accretion rates are assumed to occur at equal annual rates resulting in a stable active floodplain. Erosion rates were derived from the data collected during a study that assessed bank erosion along the Tanana River during a 20-year interval using aerial photographs taken in 1978 and comparing them with Landsat Thematic Mapper images from 1998 (Ott et al. 2001).

MODEL VALIDATION

I considered 4 general modeling instances to determine the effect of herbivory, erosion/accretion and an interaction between the two on landscape successional patterns.

I. Time Model (T) is the simplest model to replicate only the passing of successional time based on changes in density and biomass within pixels.
II. Time and Herbivory Model (T*H) incorporates a herbivory variable, which effects the willow alder and poplar biomass in the willow frame as well as successional processes from the Time Model.
III. Time and Erosion Model (T*E) which allows the river to move across the landscape simulating erosion and accretion effects in addition to the successional process.
IV. Time, Herbivory, Erosion Model (T*H*E) is a global model that incorporates all of the processes from the previous models.

The simulated landscape compositions were compared to vegetation compositions observed by Ott et al. (2001) and transect data from two study areas along the Tanana River that differed in herbivory levels and erosion/accretion levels. A model was considered valid if the simulated landscapes reflected actual patterns observed along the Tanana River. The observed vegetation compositions compared with model outputs were landscape proportion, willow to alder ratio (W:A), and willow AGB (g/m^2). The low herbivory study area had a moose density of 0.2 moose/km^2, 15% of the available stems

browsed by moose and snowshoe hares and an erosion/accretion rate of 4.2 ha/km/yr. The high herbivory area had a moose density of 0.5 to 1 moose/km^2, 69% of forage plant stems browsed by moose and hares and an erosion/accretion rate of 6.1 ha/km/yr.

HYPOTHESIS TESTING

The hypotheses were tested using 56 different combinations of erosion/accretion and herbivory levels, simulating naturally occurring variation in these parameters (Tables 2.1 and 2.2). Each model combination was replicated 100 times. The herbivory, erosion/accretion and interaction effects were evaluated based on percent landscape cover of each model frame, residence time, total AGB of willow (kg/ha) and mean willow AGB (g/m^2), where I defined residence time as the length of time a pixel is a particular frame type, total AGB as the total amount of willow above ground biomass on the landscape, and mean AGB as the average amount of willow above ground biomass within a willow pixel. Residence time was examined to distinguish between changes in landscape proportions that result from changes in successional transition rates and those that result as a consequence of another frame type becoming a larger or smaller percentage of the landscape. Total AGB of willow represents the quantity of forage available on the landscape and influences the search effort required by herbivores to find forage. Mean AGB of willow is used as an indication of the amount of forage biomass available to a herbivore within a willow stand regardless of the stand's size or the proportion of willow on the landscape.

DATA ANALYSIS

A Two-Way ANOVA was used to test the significance of herbivory (7 levels), fluvial dynamics (8 levels) and an interaction term on model parameters and was verified using Stepwise Regression. Multivariate regression models indicated whether the factors had a positive or negative influence on model parameters. All data were analyzed using SAS statistical software, SAS Institute Inc. (2001) at an α level of 0.05.

RESULTS

Model Validation

Overall the model simulated the theoretical landscape well. The model accurately followed the rules established for the simulated landscape and mimicked landscape processes observed on the Tanana River. The output of each model instance reflected changes in the landscape that conformed to theoretical expectations even though the instances did not always reflect the observed landscapes.

Model T resulted in a landscape composed of 100% trees and was rejected as a means to describe the factors controlling landscape vegetation patterns observed in the field study areas. Similarly, model T*H failed to produce new soil for colonization and resulted in a landscape of 100% trees. However, both model instances performed as expected on a theoretical landscape without abiotic factors such as erosion and accression. Without abiotic factors present to produce bare soils for colonization, the landscape would be expected to be composed entirely of late successional stages.

T*E performed better than all other instances in comparison with the low herbivory field study area (Table 2.3). However, when compared with the high herbivory area (Table 2.4), it overestimated the proportion of willow by 15.4% and the W:A ratio by 1.7, and underestimated the proportion of bare soil by 5.2% and late successional stage trees by 10.9%.

The results of model T*H*E were reasonable in comparison with the low herbivory area (Table 2.3). The greatest difference between the simulation and observed data was in the overestimation of trees by 3.3%. This instance also performed reasonably well in comparison with the high herbivory area (Table 2.4). The greatest difference in this comparison was in the proportion of bare soil on the landscape, which was underestimated by 5.8% in the model simulation. No significant differences were detected in the W:A ratio in comparisons of model T*H*E and the observed data.

Model Simulations

Landscape Proportions

Erosion/accretion had a positive effect on the proportion of bare soil on the landscape ($F_{7, 5544} = 4.68 \times 10^5$, $P < 0.001$), where increases in erosion and accretion increased the proportion of bare soil. Herbivory and the interaction between herbivory and erosion/accretion were not significant ($F_{6, 5544} = 0.14$, $P = 0.992$ and $F_{42, 5544} = 1.29$, $P = 0.102$ respectively; Figure 2.2). With herbivory held constant at the 40% level, doubling erosion/accretion from 3 ha/km to 6 ha/km increased the proportion of bare soil 215% and increased bare soil 109% when erosion/accretion was doubled again (6 ha/km to 12 ha/km).

There were significant effects of erosion/accretion, herbivory and their interaction in the willow frame ($F_{7, 5544} = 1.78 \times 10^8$, $P < 0.001$; $F_{6, 5544} = 1.70 \times 10^7$, $P < 0.001$; and $F_{42, 5544} = 2.36 \times 10^6$, $P < 0.001$ respectively; Figure 2.3) and in all of the subsequent successional frame types (Figures 2.4, and 2.5). The number of willow pixels in the simulated landscape decreased with increases in herbivory and the interaction term (Figure 2.3). With a constant erosion/accretion rate of 6 ha/km, herbivory decreased the proportion of willow on the simulated landscape 26% when increased from 20% to 40% herbivory, and decreased willow 49% when increased from 40% to 80% herbivory. With a constant herbivory level of 40%, erosion/accretion increased the number of willow pixels 180% when increased from 3 ha/km to 6 ha/km, but only increased willow pixels 98% when erosion/accretion was doubled again from 6 ha/km to 12 ha/km.

Alder abundance increased with increased erosion/accretion and the interaction term and decreased as the herbivory rate was increased ($F_{7, 5544} = 1.46 \times 10^7$, $P < 0.001$; $F_{42, 5544} = 3.71 \times 10^5$, $P < 0.001$; and $F_{6, 5544} = 5.17 \times 10^5$, $P < 0.001$ respectively; Figure 2.4). The effects of erosion/accretion can be seen throughout the range of erosion/accretion scenarios. Doubling erosion/accretion produced similar results to those described for the willow frame with increases of 195% and 98% respectively. Herbivory influenced this

frame type at high erosion/accretion levels increasing the alder proportion 1% in each of our doubling scenarios when erosion/accretion was held at 6 ha/km.

The tree frame was negatively correlated with erosion/accretion level and was positively correlated with herbivory in the willow stage and the interaction term ($F_{7, 5544} = 1.97 \times 10^7$, $P < 0.001$; $F_{6, 5544} = 6.42 \times 10^6$, $P < 0.001$; and $F_{42, 5544} = 5.61 \times 10^5$, $P < 0.001$ respectively; Figure 2.5). This frame was effected more by changes in erosion/accretion (where the proportion of trees decreased 14% when erosion/accretion was doubled from 3 ha/km to 6 ha/km and decreased 23% with an increase from 6 ha/km to 12 ha/km) than it was by herbivory (where doubling herbivory increased the proportion of tree pixels 5% in both doubling scenarios).

W:A Ratio

W:A Ratio was significantly effected by erosion/accretion, herbivory and the interaction term ($F_{7, 5544} = 1.29 \times 10^6$, $P < 0.001$; $F_{6, 5544} = 2.22 \times 10^6$, $P < 0.001$; and $F_{42, 5544} = 4.63 \times 10^5$, $P < 0.001$; Figure 2.6). Erosion/accretion was negatively correlated with the ratio, while herbivory and the interaction term were positively correlated, with the most extreme interactions occurring at high erosion/accretion and low herbivory. The W:A ratio was less sensitive to changes in erosion/accretion than to changes in herbivory. Erosion/accretion increased the W:A ratio 1% when doubled from 3 ha/km to 6 ha/km and increased 5% with an increase from 6 ha/km to 12 ha/km. Herbivory decreased the ratio 27% when increased from 20% herbivory to 40%, and decreased 61% when the herbivory level was doubled again from 40% to 80%.

Residence Times

Residence time of all model frames was significantly effected by erosion/accretion, herbivory and the interaction between the two ($P < 0.001$) with the exception of bare soil where only erosion/accretion significantly influenced residence time ($F_{7, 5544} = 951.99$, $P < 0.001$, Figure 2.7). Erosion/accretion had a negative effect on frame duration after

erosion/accretion levels were increased to a sufficient level to produce bare soil on the simulated landscape. Herbivory decreased residence time of the willow frame (Figure 2.8) and increased the residence time of the alder and tree frames (Figures 2.9 and 2.10). Residence time in all model variations averaged 1.2 yrs (S.E. = 1.0) in the bare soil frame, 43.7 yrs (S.E. = 2.8) in the willow frame, 31.7 yrs (S.E. = 0.6) in the alder frame, and 118.7 yrs (S.E. = 8.1) in the tree frame. Tree residence time increased as the number of years modeled increased, and is given here as a reference point for the other model frames.

Willow Above Ground Biomass

Total willow AGB on the simulated landscape (kg/ha) and mean willow AGB per pixel (g/m^2) were significantly effected by erosion/accretion, herbivory, and the interaction term ($F_{7, 5544} = 1.45 \times 10^7$, $P < 0.001$; $F_{6, 5544} = 2.43 \times 10^7$, $P < 0.001$; and $F_{42, 5544} = 1.16 \times 10^6$, $P < 0.001$ and $F_{7, 5544} = 5.64 \times 10^7$, $P < 0.001$; $F_{6, 5544} = 5.31 \times 10^7$, $P < 0.001$; and $F_{42, 5544} = 7.50 \times 10^6$, $P < 0.001$ respectively; Figures 2.11 and 2.12). Total AGB was positively correlated with erosion/accretion and negatively correlated with herbivory and the interaction term (Figure 2.11). Erosion/accretion increased total AGB 196% when doubled from 3 ha/km to 6 ha/km and increased total AGB 97% when erosion/accretion was increased again from 6 ha/km to 12 ha/km. Total AGB was decreased 55% when herbivory levels were changed from 20% to 40% and decreased 90% when herbivory was increased again from 40% to 80%. Mean AGB (g/m^2) was negatively correlated with erosion/accretion and herbivory and positively correlated with the interaction term (Figure 2.12). R^2 values increased from 0.587 to 0.984 with the removal of the extremely low erosion/accretion levels (0 ha/km and 0.04 ha/km) in which the landscape was 100% trees, completely lacking in willow, and changed little with the removal of erosion/accretion and the interaction term ($R^2 = 0.982$) indicating that the effect of erosion/accretion was minimal on this scale of biomass. Erosion/accretion decreased mean AGB by less than 1% in all doubling scenarios, while herbivory decreased mean

AGB by 39% when doubled from 20% to 40% and decreased mean AGB 83% when doubled again from 40% to 80%.

DISCUSSION

Abiotic and biotic factors influence successional patterns and modify the proportions of plant communities on the landscape. The abiotic factors (erosion and accretion) played a major role in shifting the landscape towards early successional communities, while biotic factors acted in the opposite direction, shifting landscapes toward later successional communities. The resulting landscape patterns reflect the combined effects of these two factors.

The comparison of model instances shows the importance of biotic and abiotic factors. Models T and T*H followed successional patterns reasonably well, but failed to produce bare soils for plants to colonize resulting in landscapes with 100% tree cover. Model T*E produced a landscape that tracked plant succession well and produced a good estimate of landscape vegetation patterns when compared with natural stands exposed to low herbivory. However, this model instance performed poorly when compared to a natural landscape exposed to high levels of herbivory. Overall, model T*H*E performed better than the alternate models when compared with landscapes exposed to varying herbivory levels. Its poorer performance in comparison with low herbivory areas is likely due to the minor influence of herbivory in changing successional processes at low herbivory levels. This validation exercise identified model T*H*E as the best model for simulating riparian successional processes.

The simulation model consistently underestimated the amount of bare soil formed in the high herbivory area in all model instances. This difference between simulated and observed values is due to changes in river water level during the course of a year, making it difficult to estimate the percent of bare soil in a landscape and I do not think it is an inherent problem with the model. Differences also result from the transient nature of

bare soil along the Tanana River, in which soil can be deposited but erodes before it is colonized by plants. Increasing the amount of bare soil created by the river in the model would inflate the proportion of shrub communities in the landscape above naturally occurring levels and can only be done by artificially inflating the observed erosion and accretion rates reported by Ott et al. (2001). Therefore, it is best to associate the percentage of bare soil in the model with the percentage of soil that can be colonized in naturally occurring landscapes and not with what is observed at any one point in time during the course of a year.

The W:A ratio is likely the best point of comparison for the simulated model and the observed landscape since it is the least sensitive to changes in the simulated river size and shape. Sensitivity testing indicated that increasing the size of the river lowers the proportion of trees on the landscape and increases the proportion of willow and alder, due to the fact that willow and alder have a shorter duration on the landscape and trees only transition to other frames through erosion in the current model. The W:A ratio is not effected by changes in the river since it is a relative measure of the landscape. For example, when testing the model, changing the width of the river from 60 m to 300 m increased the willow and alder proportions by less than 2% and decreased the tree proportion by 3.9%, and did not effect the W:A ratio. It is important to note that this modeling exercise does not incorporate the effects of braided river channels and island dynamics. Additionally, the willow to alder ratio is a measure of habitat for mammalian herbivores that utilize both of these tall shrub communities for cover (Collins and Helm 1997, Weixelman et al. 1998) and is thereby considered an important parameter in this model.

The W:A ratio resulting from model T*H*E corresponds well with the transect surveys. I found that on a per area basis the willow to alder ratio in the high moose density area was 0.8 and 1.9 in the low density area. In the model, the willow to alder ratio predicted for these areas was 0.8 and 1.8 respectively, indicating that herbivory is an important

factor shaping the abundance and distribution of vegetation communities in the landscape.

The selection of model T*H*E and the importance of erosion, herbivory, and interaction under a wide range of biotic and abiotic combinations support the hypothesis that biotic and abiotic factors change landscape vegetation patterns, and their interactions effect the landscape in ways that are not explainable by either factor alone.

Erosion/accretion, herbivory and their interaction were significant in both ANOVA and stepwise regression tests of distribution data, with the exception of the proportion of bare soil in the landscape in which only erosion was an important factor. It becomes apparent that changes in the number of pixels of one frame type by necessity changes the number of pixels in following successional stages since there are a finite number of pixels in the simulated landscape. Whereas this is ultimately important biologically, since organisms typically deal with spatial limitations, it does not necessarily illustrate the mechanism by which these changes occur. Residence time was used to look at changes more critically to determine if a change in transition frequency is being modified in a particular frame type.

Erosion/accretion had a negative effect on frame duration after erosion/accretion levels were increased to a sufficient level to produce bare soil on the simulated landscape. Herbivory had a negative effect on residence time in the willow frame (Figure 2.8) and positive effects on the residence time in the alder and tree frame (Figures 2.9 and 2.10). The negative effects of herbivory in the alder and tree frame are likely attributable to the increased duration of the willow frame causing younger tree frames to be eroded by the river. This is supported by the effects of herbivory being seen only under the high erosion/accretion scenarios in the willow and alder frames, while the effects are readily seen in the tree frames even at low erosion/accretion levels.

Differences in residence times between model results and the minimum age of natually occurring stands, determined by the number of growth rings of individual plants, were noted in willow. Felt leaf willow (*Salix alaxensis*) have been observed with up to 46 annual growth rings (Bliss et al. 1957, Binkley et al. 1997). Similarly, Helm and Collins (1997) documented some early shrub communities to have existed for 44 years using aerial photographs. Nonetheless, there is a lack of old willow stands reported in the literature as predicted by this model. It is likely that there is an upper limit on the potential age of any one plant, and assessing stand age using the maximum age of plants observed at each stand likely results in a conservative estimate and produces a bias towards lower stand age estimates. The bias towards lower stand ages is due to the potential for older plants to be removed before plant ages are sampled to determine stand age and due to the quick transition from bare soil sparely populated by willow to a willow community. Old willow stands may also be limited by willow mortality, and a replacement of individuals by later successional species constituting a life-history constraint on willow stand age. The residence times of the alder frames in this model were in the range observed in several studies that reported ages of 22 to 33 years (Helm and Collins 1997 and Van Cleve et al. 1993)

The hypothesis that willow biomass on the landscape was influenced by herbivory was supported by both total and mean AGB. Erosion/accretion effected total AGB, presumably through the creation of more bare soil at high accretion levels, but was not important in mean AGB, which estimates production within a willow community, until the high erosion/accretion values were used (Figure 2.12). The effects of erosion/accretion in the model were attributable to the slow generation of willow in low erosion/accretion and the removal of willow before it was fully developed in the high erosion/accretion scenario. This implies that the erosion/accretion factor in this model can influence successional patterns by reverting communities to earlier successional stages and that the erosion/accretion factor performed as expected.

I conclude that the simulation model mimicked landscape processes accurately enough to evaluate the effect of biotic and abiotic factors on landscape vegetation dynamics. Erosion/accretion was a major factor in all vegetation communities and parameters evaluated in this modeling exercise. Herbivory played a relatively minor role in influencing landscape vegetation patterns at low erosion and accretion levels, but had a large effect in combination with high levels of erosion and accretion. Herbivores do influence their environment, and herbivory should therefore be incorporated into models simulating riparian landscapes exposed to high herbivory levels.

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WOLFF, J.O., AND J.C. ZASADA. 1979. Moose habitat and forest succession on the Tanana River flood plain and Yukon-Tanana upland. Pages 213-244. *In* H.G. Cumming (*ed.*) Proceedings of the North American moose conference and workshop 15. Ontario Department of Lands and Forests, Thunderbay, Ontario, Canada.

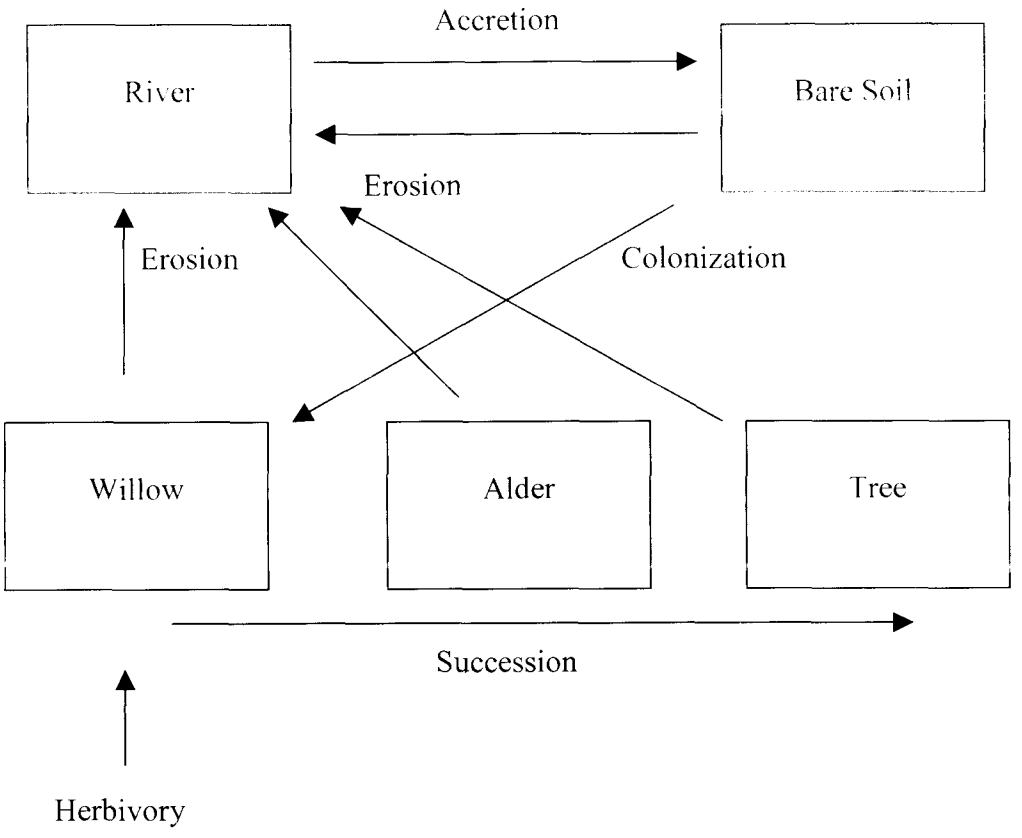


Figure 2.1. Conceptual diagram of model frames showing the mechanisms that can affect each successional stage.

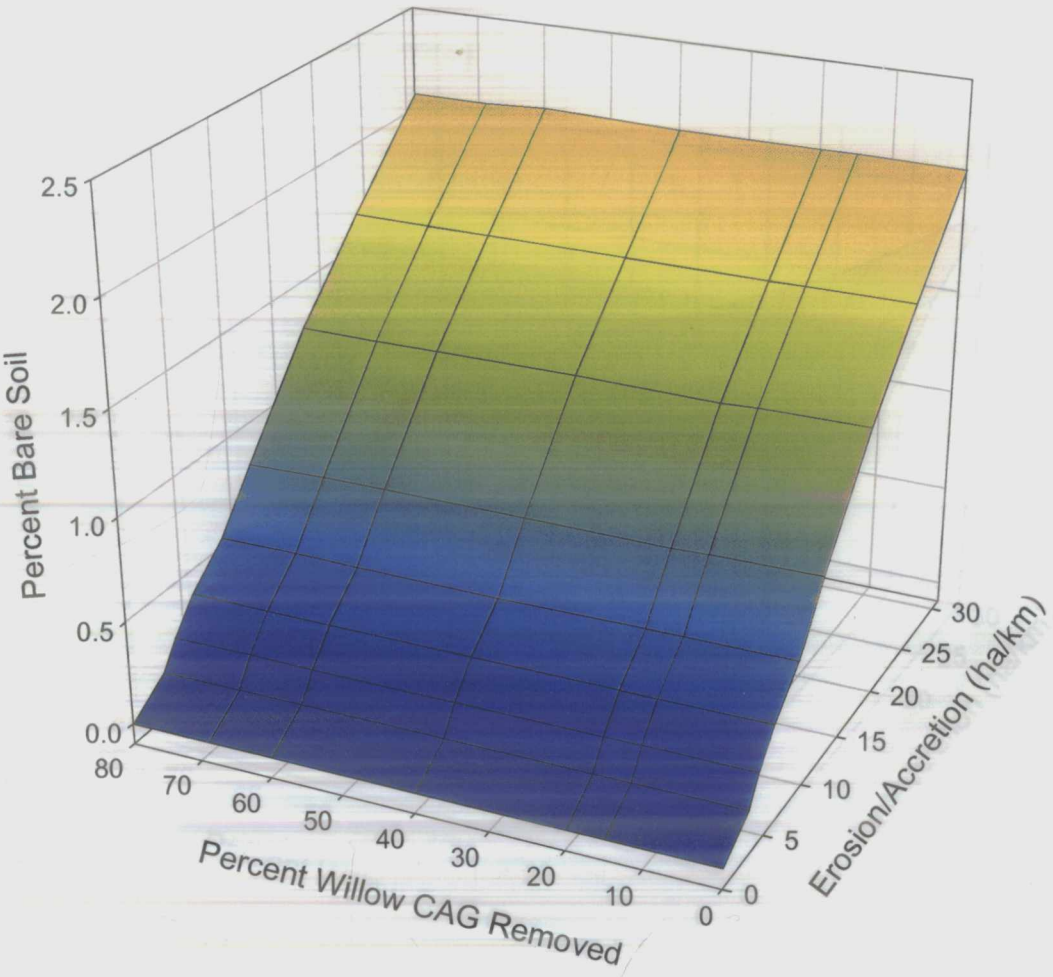


Figure 2.2. Percentage of the simulated landscape in the bare soil frame during year 250 of the model resulting from different combinations of erosion/accretion and herbivory. Note that graph axes may change direction in Figures 2.2 to 2.12 for readability.

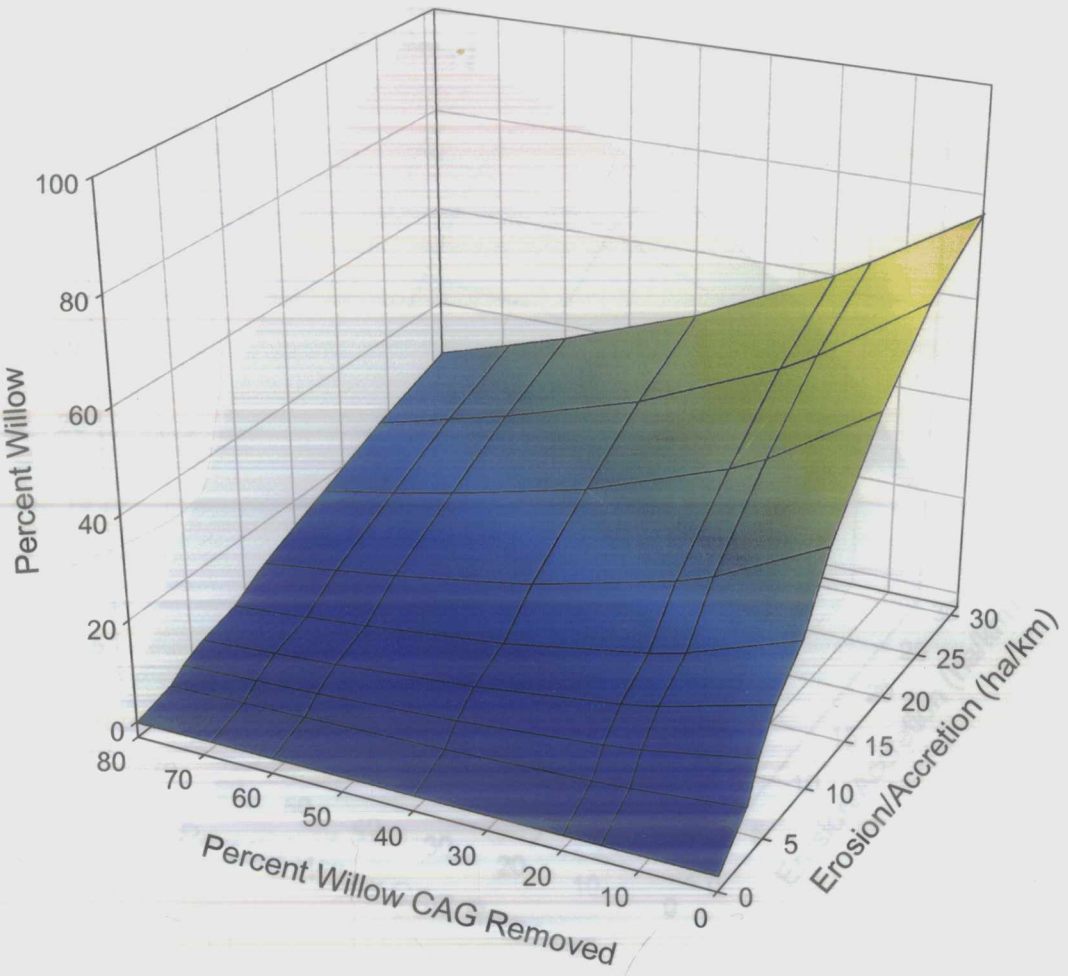


Figure 2.3. Percentage of the simulated landscape in the willow stage frame during year 250 of the model resulting from different combinations of erosion/accretion and herbivory. Note that graph axes may change direction in Figures 2.2 to 2.12 for readability.

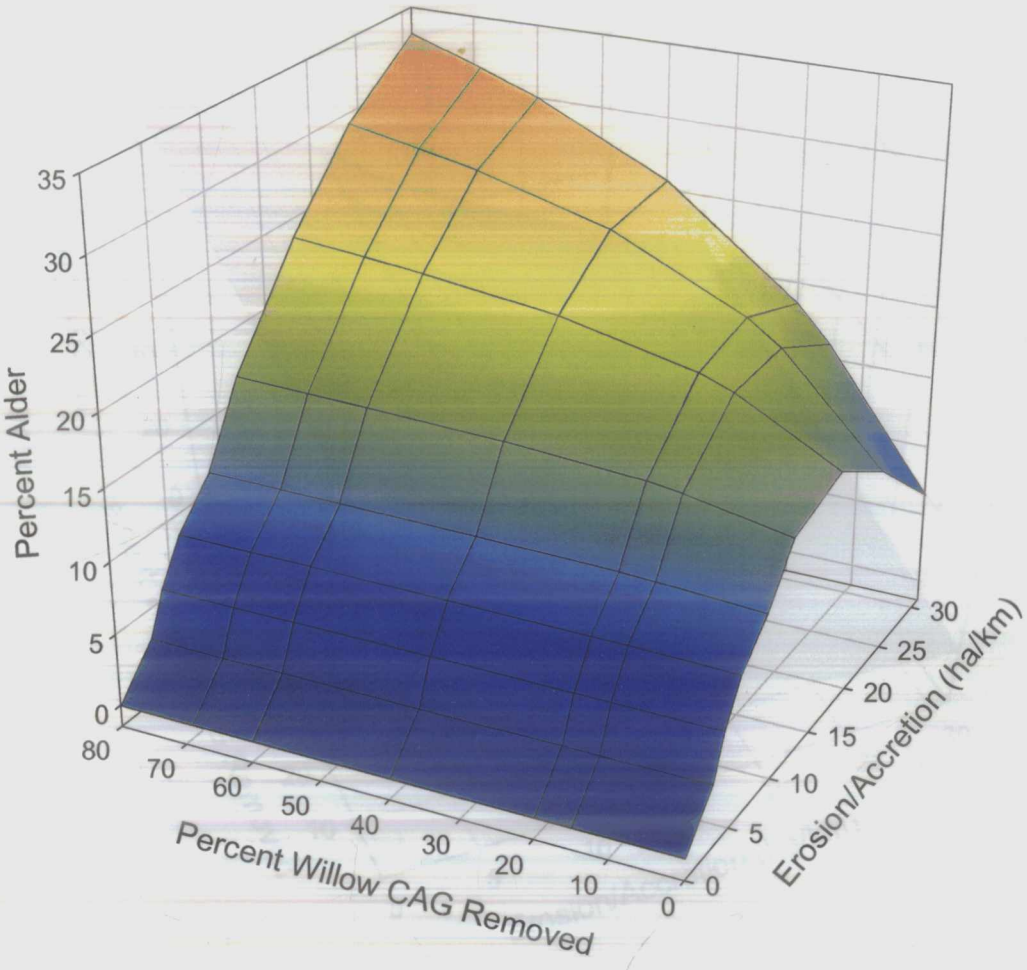


Figure 2.4. Percentage of the simulated landscape in the alder frame during the year 250 of the model resulting from different combinations of erosion/accretion and herbivory. Note that graph axes may change direction in Figures 2.2 to 2.12 for readability.

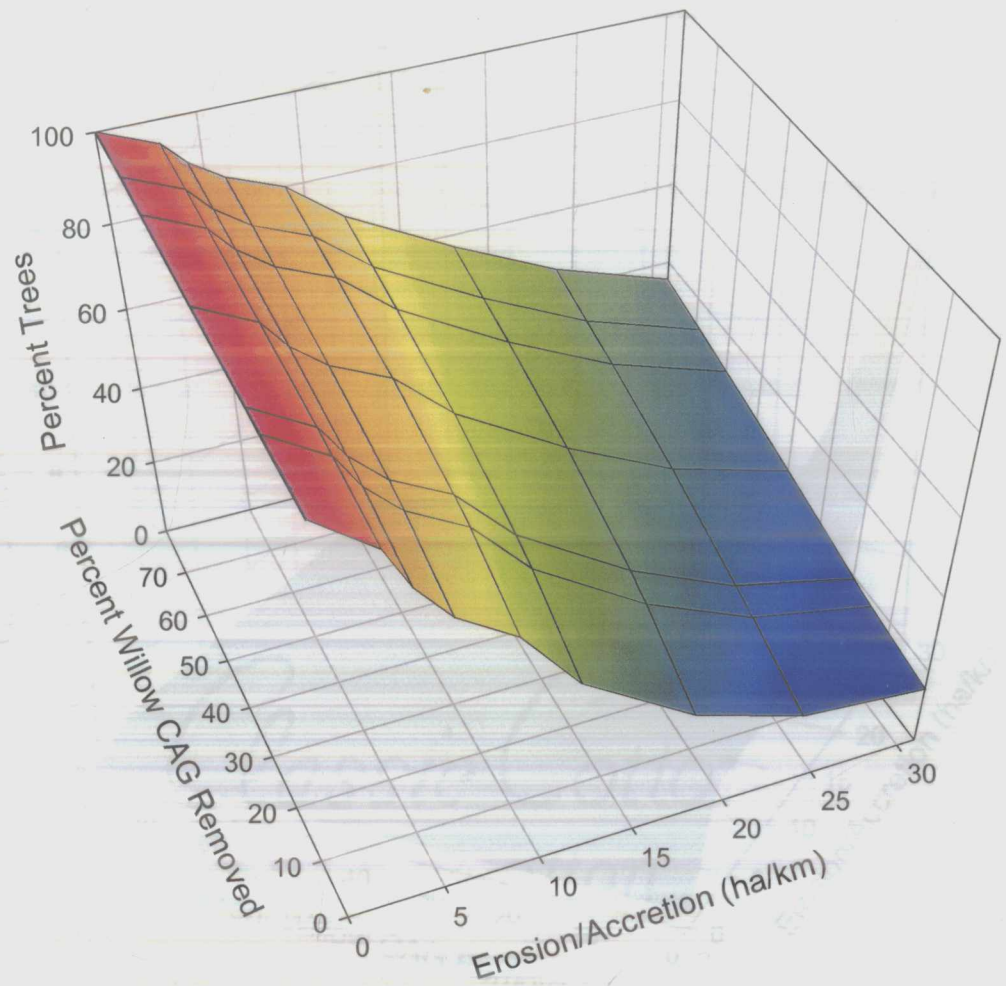


Figure 2.5. Percentage of the simulated landscape in the tree frame during year 250 of the model resulting from different combinations of erosion/accretion and herbivory. Note that graph axes may change direction in Figures 2.2 to 2.12 for readability.

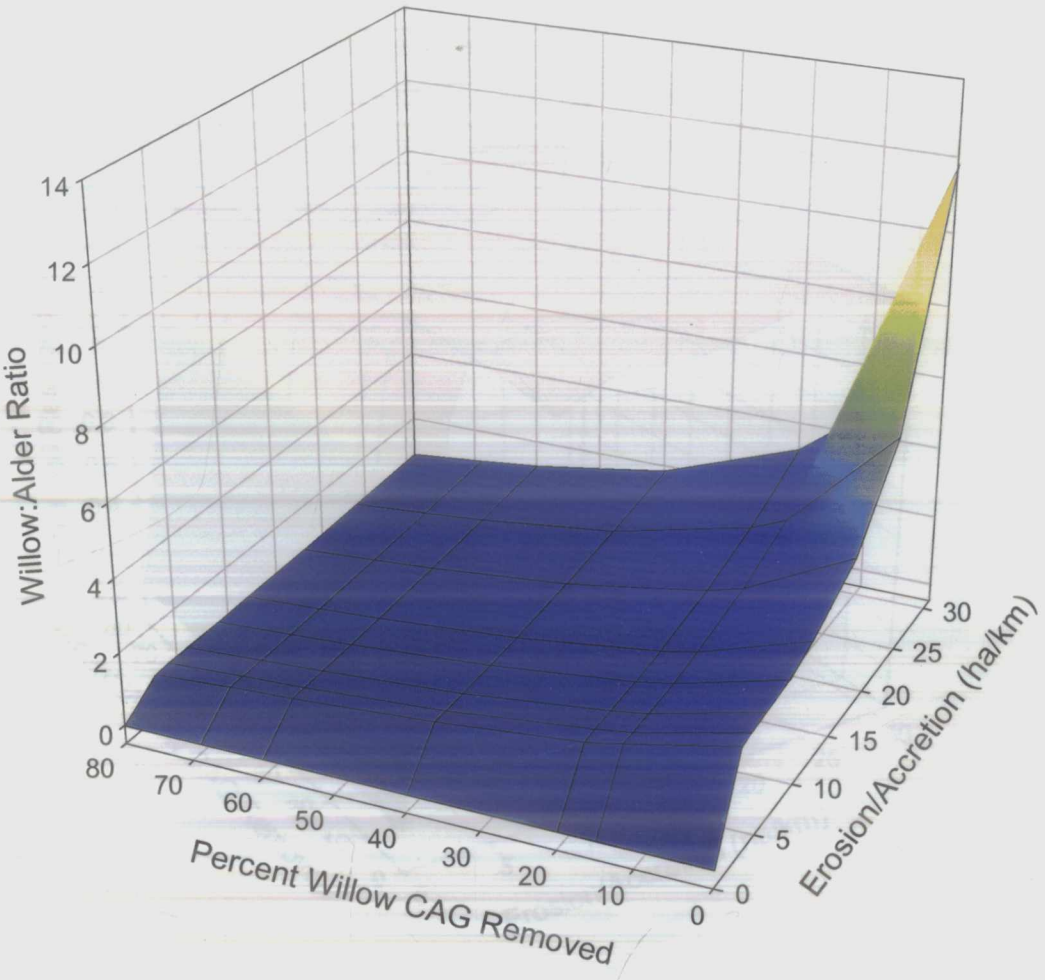


Figure 2.6. Ratio of willow to alder frames in the simulated landscape during year 250 of the model resulting from the simulated herbivory and erosion/accretion scenarios. Note that graph axes may change direction in Figures 2.2 to 2.12 for readability.

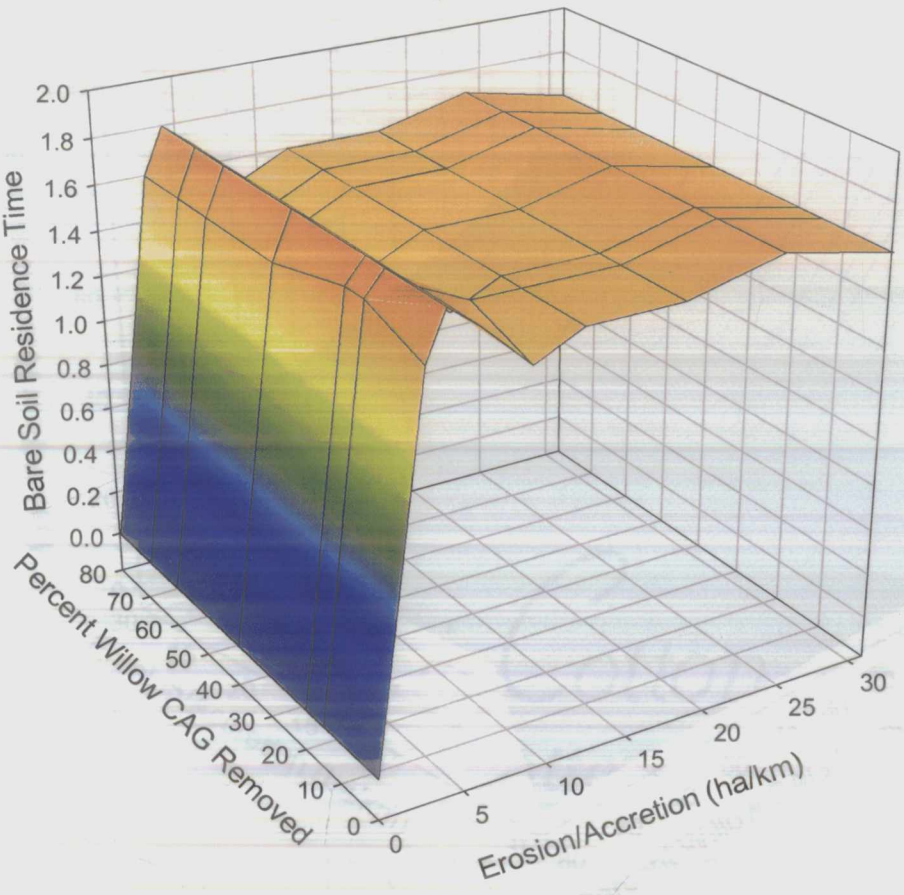


Figure 2.7. Average residence time (yrs) of the bare soil frame during year 250 of the model resulting from the simulated herbivory and erosion/accretion scenarios. Note that graph axes may change direction in Figures 2.2 to 2.12 for readability.

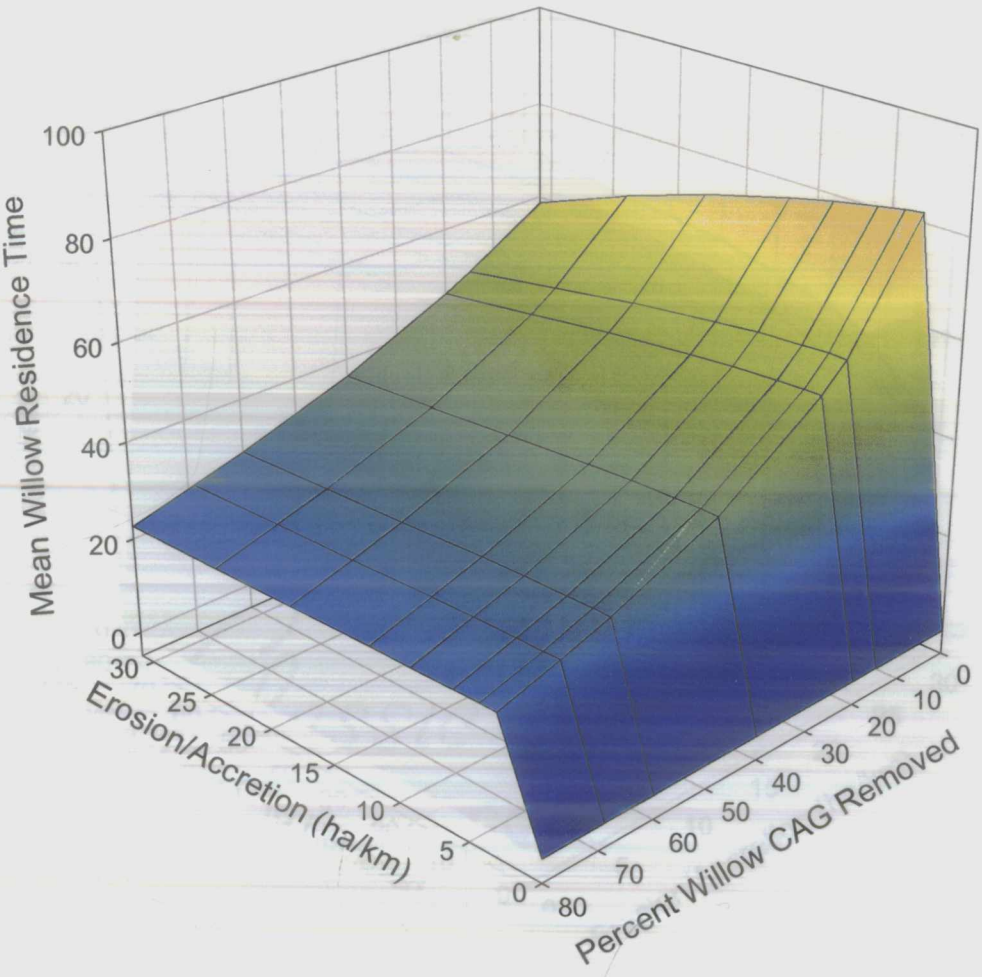


FIGURE 2.8. Average residence time (yrs) of the willow frame during year 250 of the model resulting from the simulated herbivory and erosion/accretion scenarios. Note that graph axes may change direction in Figures 2.2 to 2.12 for readability.

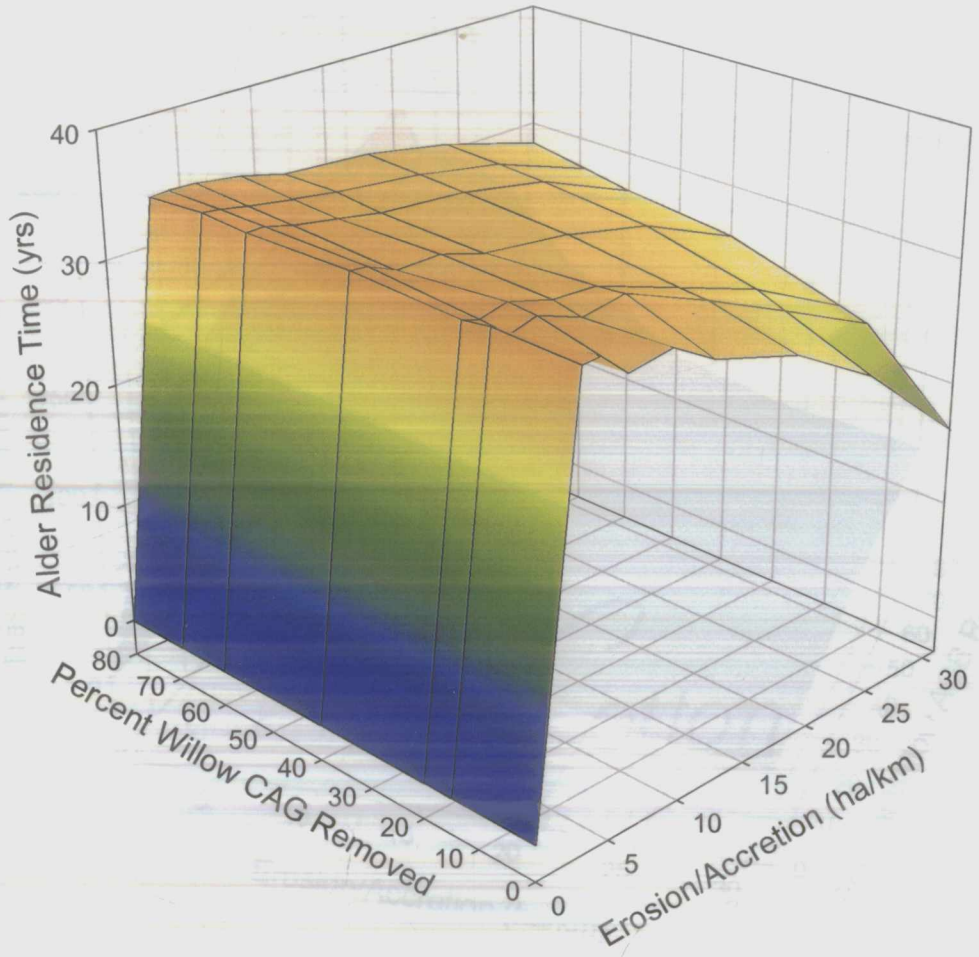


FIGURE 2.9. Average residence time (yrs) of the alder frame during year 250 of the model resulting from the simulated herbivory and erosion/accretion scenarios. Note that graph axes may change direction in Figures 2.2 to 2.12 for readability.

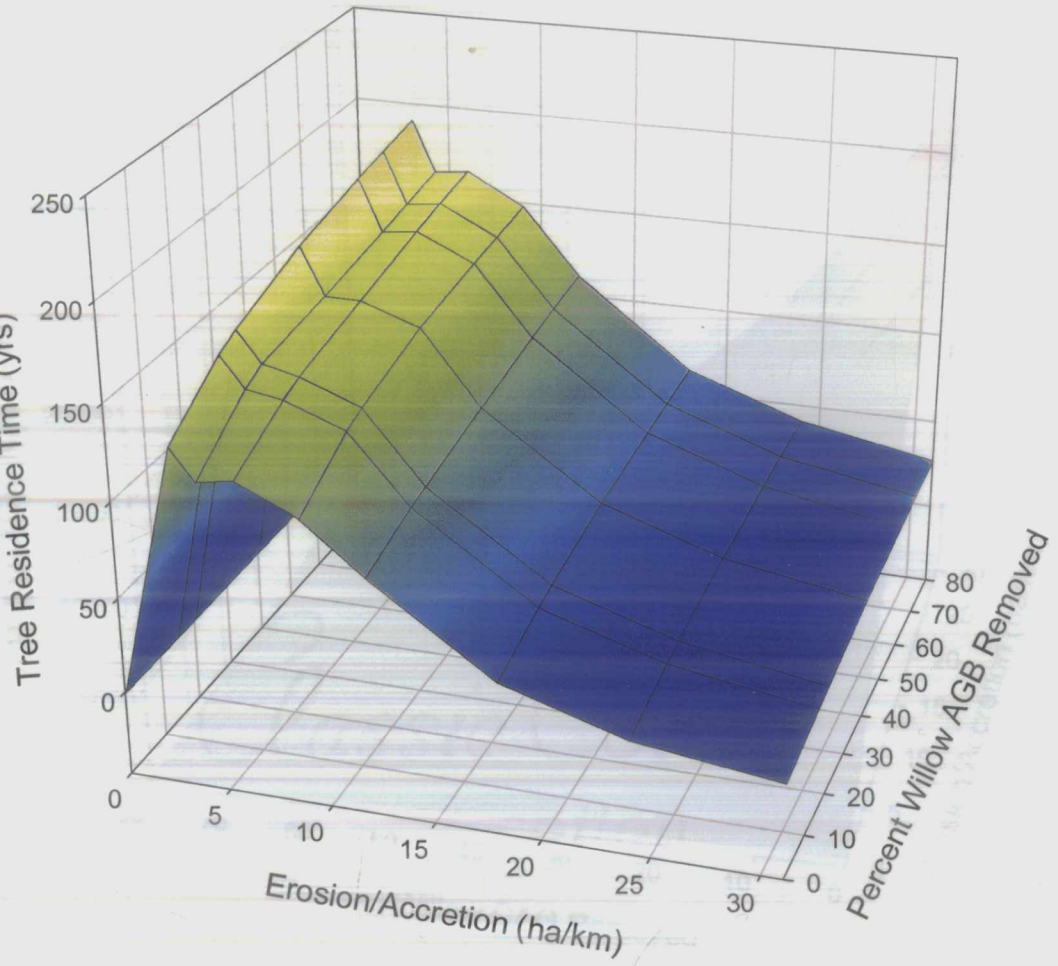


FIGURE 2.10. Average residence time (yrs) of the tree frame during year 250 of the model resulting from the simulated herbivory and erosion/accretion scenarios. Note that graph axes may change direction in Figures 2.2 to 2.12 for readability.

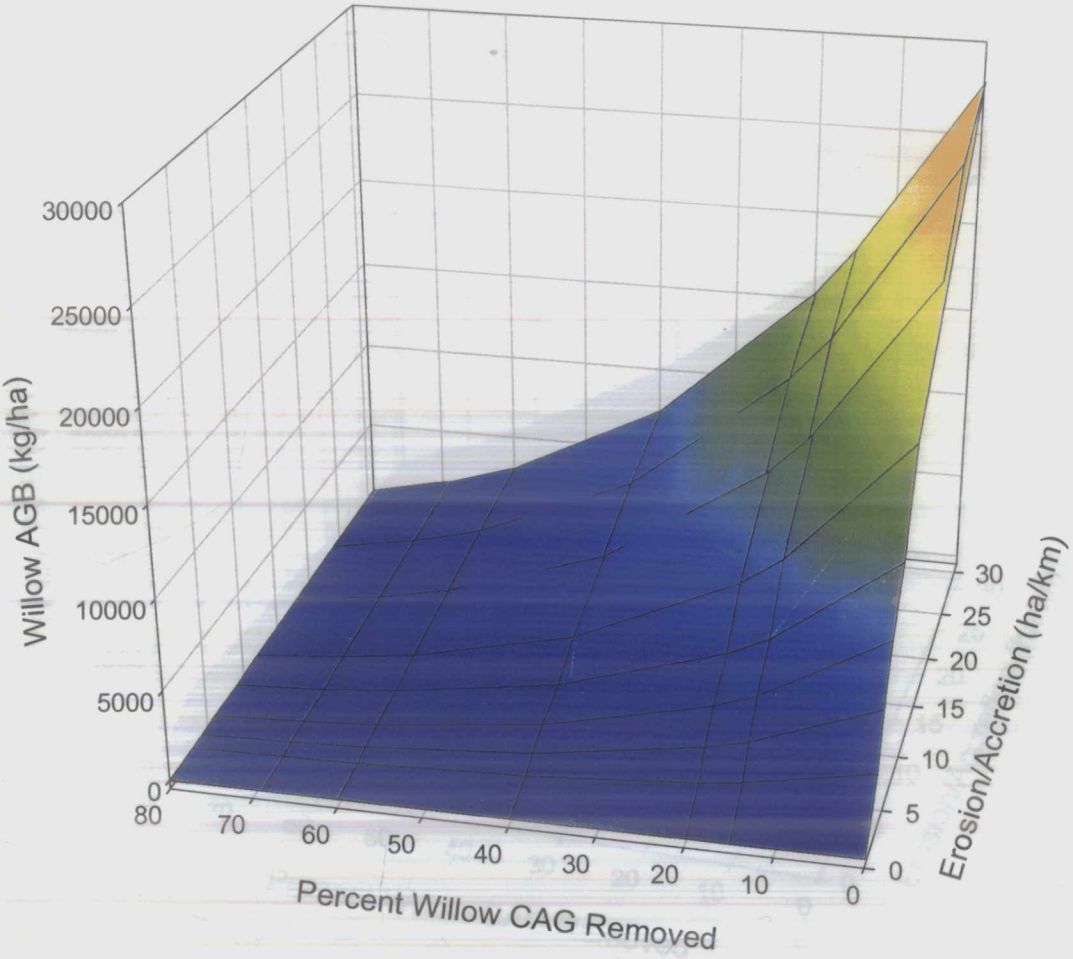


Figure 2.11. Total willow above ground biomass during year 250 of the model resulting from the simulated herbivory and erosion/accretion scenarios. Note that graph axes may change direction in Figures 2.2 to 2.12 for readability.

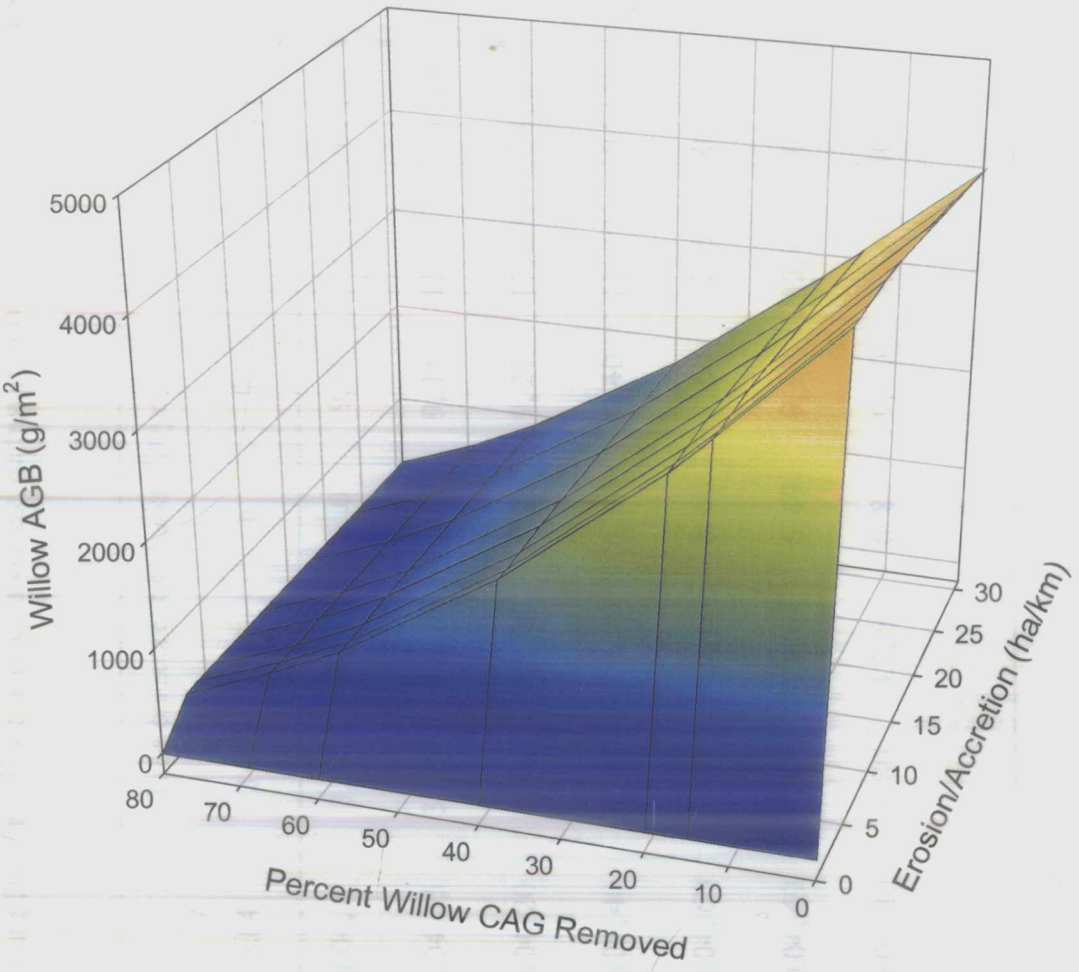


FIGURE 2.12. Willow above ground biomass per m^2 in willow communities during year 250 of the model resulting from the simulated herbivory and erosion/accretion scenarios. Note that graph axes may change direction in Figures 2.2 to 2.12 for readability.

Table 2.1. Model testing design showing the combinations of erosion and herbivory levels used to test hypotheses.

		Erosion/accretion (ha/km/20yr)							
		0	0.04	3	4.2	6	9	12	30.9
Herbivory	0%	0, 0	0.04, 0	3, 0	4.2, 0	6, 0	9, 0	13, 0	30.9, 0
	15%	0, 15	0.04, 15	3, 15	4.2, 15	6, 15	9, 15	13, 15	30.9, 15
	20%	0, 20	0.04, 20	3, 20	4.2, 20	6, 20	9, 20	13, 20	30.9, 20
	40%	0, 40	0.04, 40	3, 40	4.2, 40	6, 40	9, 40	13, 40	30.9, 40
	60%	0, 60	0.04, 60	3, 60	4.2, 60	6, 60	9, 60	13, 60	30.9, 60
	69%	0, 69	0.04, 69	3, 69	4.2, 69	6, 69	9, 69	13, 69	30.9, 69
	80%	0, 80	0.04, 80	3, 80	4.2, 80	6, 80	9, 80	13, 80	30.9, 80

Table 2.2. Erosion/accretion values used to simulate erosion/accretion along the Tanana River. Model river movement reflects the distance the river advanced across the simulated landscape each year under different erosion/accretion scenarios.

Modeled Erosion/Accretion Scenarios	Observed Erosion/Accretion (ha/km/20yr)	Model River Movement (m/pixel/yr)
Zero Erosion/Accretion	0	0
Minimal Erosion/Accretion	0.03*	0.02
Low Erosion/Accretion	3.0	1.5
Low Herbivory Area	4.2*	2.1
High Herbivory Area	6.1*	3.0
Average Erosion/Accretion	6.2*	3.1
Intermediate	9	4.5
Medium	12.0	6
High Erosion/Accretion	30.9*	15.5

*Values reported by Ott et al. (2001) after conversion from ha/10km/20yrs.

Table 2.3. Comparison of landscape proportions for the 15% herbivory study area with the equivalent simulation data used to validate the model. Standard Errors were < 0.007 in all cases, making differences < 0.2 significant.

	Observed	Model T	Model T*H	Model T*E	Model T*H*E
Bare Soil	0.1	0	0	0.2	0.2
Willow	12.7	0	0	13.9	10.1
Alder	6.6	0	0	5.7	5.7
W:A Ratio	1.9	N/A	N/A	2.4	1.8
Tree	80.6	100	100	80.2	83.9
χ^2 , df = 3		24.1	24.1	0.3	0.9

Table 2.4. Comparison of landscape proportions for the 69% herbivory study area with the equivalent simulation data used to validate the model. Standard Errors were < 0.007 in all cases making differences < 0.2 significant.

	Observed	Model T	Model T*H	Model T*E	Model T*H*E
Bare Soil	6.2	0	0	0.4	0.4
Willow	5.3	0	0	20.7	7.0
Alder	6.8	0	0	8.2	8.6
W:A Ratio	0.8	N/A	N/A	2.5	0.8
Tree	81.6	100	100	70.7	84.0
χ^2, df = 3		22.4	22.4	51.9	6.5

SYNOPSIS AND CONCLUSION

Moose and snowshoe hares fed on willow species and poplar in willow communities along the Tanana River during the winter. Herbivores primarily selected *S. alaxensis*, *S. lasiandra*, *S. novae-angliae*, and *P. balsamifera* L. Changes in browsing intensity significantly affected willow communities on both the plot and landscape levels. Willow communities subject to heavy browsing had a shorter overall canopy height. Browsing further reduced the canopy height in the high moose density area during the winter months.

Study sites in both areas were composed primarily of willow, with *S. alaxensis* the dominant species. High levels of herbivory resulted in greater plant mortality, but had no effect on the density of plant species within the communities. Dead plants appear to be replaced quickly by new shoots in these highly productive communities.

The total carbon and nitrogen stores in the soil were lower in heavily browsed stands, but the differences were not attributed to herbivory. Soil nutrient levels were correlated with the amount of organic material found in the soils. The shallower organic layer and lower concentrations of soil nutrients in the high moose density area may be the result of the younger age of the soils, increased nutrient turnover rates, decreased fine root production, leaching following flooding events, and a reduction in leaf litter fall as a result of leaf stripping by herbivores during the summer (Kielland et al. 1997).

The average ages of *S. alaxensis*, *S. lasiandra*, and *S. novae-angliae* were younger in willow communities exposed to high herbivory levels, and the oldest detected stand age of willow communities was younger in communities exposed to high herbivory levels. The lack of differences in the age distribution of alder between the high and low density areas, in spite of the older age of willow in the low browsing intensity area, implies a delay in alder colonization. This difference combined with differences in overall stand

age between the two areas suggests a quicker successional transition from willow to alder in heavily browsed areas

Similarly, the high herbivory area had fewer willow communities than the low herbivory area, and communities were smaller in size, in spite of the higher rates of erosion/accretion found along this section of river. Increased erosion and accretion rates should produce more soils for willow to colonize increasing the number of willow communities. Furthermore, a greater proportion of the shrub communities were dominated by alder in the high density area. This implies that herbivory shifts the landscape vegetation composition toward later successional stages.

The frame-based model, designed to incorporate the stand level findings of this study, supported these conclusions. Simulated landscapes, resulting from the herbivory and erosion/accretion levels of the study areas, were evaluated based on how closely they reflected the actual field site data. The model containing herbivory and erosion/accretion parameters (Model T*H*E) most closely approximated the actual landscape in high herbivory areas, while the model allowing for erosion and accretion without herbivory (Model T*E) corresponded well with the low herbivory area. Models with herbivory more accurately reflected the ratio of willow to alder communities found along the Tanana River. This exercise not only validated the model, but supports the hypothesis that herbivory is important in determining landscape distribution patterns.

Closer examination of the model indicated that herbivory acted as an antagonist to erosion/accretion in model simulations. While erosion/accretion shifted the simulated landscape toward early successional communities, herbivory shifted the landscape toward later successional stages. Interactions between erosion/accretion and herbivory significantly effected all successional frame types with the exception of bare soil. The combination of low herbivory and high erosion/accretion had the greatest effect in reverting early successional stages back to the river frame, while high herbivory and low

erosion/accretion resulted in a simulated landscape dominated by late successional communities. Increased herbivory was also predicted to decrease the quantity of forage biomass on the landscape. This decrease reflected the decrease in willow biomass per m^2 combined with the decrease in the amount of willow on the simulated landscape.

These findings support the hypothesis that herbivores reduce the abundance of willow communities on the landscape by altering successional turnover rates and subsequently alter landscape vegetation patterns.

APPENDIX A. LOCATIONS OF FIELD STUDY SITES AND THE SHRUB COMMUNITIES IDENTIFIED ON 21 KM TRANSECTS IN THE TWO STUDY AREAS

Index

List of Tables

Introduction

The following tables are summaries of the locations of the field study sites and the shrub communities identified on the Tanana River on the 21km transects in the 2 study areas. This information is provided to document the location of communities observed during the summer of 2001 and 2002.

Table A.1. Location of study sites in the high and low density moose areas along the Tanana River, Alaska 2001. Latitude and longitude are expressed in the WGS 84 datum.

Study Area	Site Id	Latitude	Longitude
High Density	F1	N 64° 41.35	W 148° 14.40
High Density	F2	N 64° 38.53	W 148° 21.37
High Density	F3	N 64° 39.23	W 148° 21.39
High Density	F4	N 64° 39.14	W 148° 28.44
High Density	F5	N 64° 38.46	W 148° 34.20
High Density	F6	N 64° 38.07	W 148° 39.51
High Density	F7	N 64° 35.04	W 148° 40.54
High Density	F9	N 64° 35.06	W 148° 43.05
High Density	F11	N 64° 34.32	W 148° 47.37
High Density	F12	N 64° 34.22	W 148° 58.51
High Density	F13	N 64° 40.29	W 148° 15.46
High Density	F14	N 64° 40.56	W 148° 16.18
High Density	F15	N 64° 41.06	W 148° 16.06
Low Density	M1	N 64° 58.20	W 150° 38.09
Low Density	M2	N 64° 58.11	W 150° 32.33
Low Density	M3	N 64° 58.06	W 150° 30.32
Low Density	M4	N 64° 58.08	W 150° 27.55
Low Density	M5	N 64° 57.09	W 150° 25.24
Low Density	M6	N 64° 57.03	W 150° 43.35
Low Density	M7	N 64° 57.25	W 150° 46.46
Low Density	M8	N 64° 52.10	W 150° 19.03
Low Density	M9	N 64° 55.34	W 150° 20.43
Low Density	M10	N 64° 55.55	W 150° 22.36
Low Density	M11	N 64° 57.15	W 150° 25.46
Low Density	M12	N 64° 57.28	W 150° 45.37

Table A.2. Locations of shrub communities on 21 km transects in the high and low moose density study areas along the Tanana River, Alaska 2002. Latitude and longitude are expressed in the WGS 84 datum.

ID Number	Study Area	Community Type	Location on River	Latitude	Longitude
1	High Density	Willow	North Bank	N 64° 41 53	W 148° 14 42
2	High Density	Alder	North Bank	N 64° 41 53	W 148° 14 42
3	High Density	Alder	South Bank	N 64° 41 47	W 148° 15 11
4	High Density	Willow	South Bank	N 64° 40 56	W 148° 16 21
5	High Density	Willow	South Bank	N 64° 40 56	W 148° 16 21
6	High Density	Willow	South Bank	N 64° 41 38	W 148° 16 47
7	High Density	Alder	South Bank	N 64° 41 38	W 148° 16 47
8	High Density	Alder	South Bank	N 64° 41 38	W 148° 16 47
9	High Density	Willow	North Bank	N 64° 40 34	W 148° 17 07
10	High Density	Alder	North Bank	N 64° 40 34	W 148° 17 07
11	High Density	Alder	North Bank	N 64° 40 25	W 148° 17 23
12	High Density	Willow	North Bank	N 64° 40 15	W 148° 18 17
13	High Density	Alder	South Bank	N 64° 40 15	W 148° 18 17
14	High Density	Alder	South Bank	N 64° 39 58	W 148° 18 19
15	High Density	Alder	North Bank	N 64° 39 58	W 148° 18 19
16	High Density	Alder	Island	N 64° 39 58	W 148° 18 19
17	High Density	Willow	Island	N 64° 39 58	W 148° 19 40
18	High Density	Willow	Island	N 64° 39 58	W 148° 19 40
19	High Density	Alder	Island	N 64° 39 58	W 148° 19 40
20	High Density	Willow	North Bank	N 64° 39 21	W 148° 21 09
21	High Density	Alder	North Bank	N 64° 39 21	W 148° 21 09
22	High Density	Willow	Island	N 64° 39 47	W 148° 22 55
23	High Density	Alder	Island	N 64° 39 47	W 148° 22 55
24	High Density	Willow	Island	N 64° 39 37	W 148° 23 25
25	High Density	Willow	North Bank	N 64° 39 35	W 148° 23 34
26	High Density	Alder	South Bank	N 64° 39 47	W 148° 25 30
27	High Density	Alder	North Bank	N 64° 39 44	W 148° 26 26
28	High Density	Willow	North Bank	N 64° 39 20	W 148° 27 52
29	High Density	Alder	North Bank	N 64° 39 13	W 148° 28 07
30	High Density	Alder	North Bank	N 64° 39 19	W 148° 29 55
31	High Density	Willow	South Bank	N 64° 39 12	W 148° 31 18
32	High Density	Alder	South Bank	N 64° 39 12	W 148° 31 18
33	Low Density	Willow	South Bank	N 64° 56 17	W 150° 24 23
34	Low Density	Willow	North Bank	N 64° 56 39	W 150° 25 13
35	Low Density	Alder	North Bank	N 64° 56 39	W 150° 25 13
36	Low Density	Willow	North Bank	N 64° 57 09	W 150° 25 23
37	Low Density	Willow	North Bank	N 64° 57 13	W 150° 25 36
38	Low Density	Alder	North Bank	N 64° 56 49	W 150° 25 41
39	Low Density	Willow	North Bank	N 64° 57 04	W 150° 25 55
40	Low Density	Alder	North Bank	N 64° 57 04	W 150° 25 55
41	Low Density	Willow	South Bank	N 64° 57 09	W 150° 25 59
42	Low Density	Alder	South Bank	N 64° 57 09	W 150° 25 59

Table A.2 (continued). Locations of shrub communities on 21 km transects in the high and low density study areas along the Tanana River, Alaska 2002. Latitude and longitude are expressed in the WGS 84 datum.

ID Number	Study Area	Species	Location	Latitude	Longitude
43	Low Density	Willow	South Bank	N 64° 57 32	W 150° 27 21
44	Low Density	Willow	Island	N 64° 57 35	W 150° 27 25
45	Low Density	Alder	Island	N 64° 57 37	W 150° 27 34
46	Low Density	Willow	Island	N 64° 57 51	W 150° 28 16
47	Low Density	Alder	Island	N 64° 57 51	W 150° 28 16
48	Low Density	Willow	Island	N 64° 58 45	W 150° 30 19
49	Low Density	Willow	South Bank	N 64° 58 48	W 150° 31 22
50	Low Density	Alder	South Bank	N 64° 58 48	W 150° 31 22
51	Low Density	Willow	South Bank	N 64° 58 20	W 150° 32 49
52	Low Density	Alder	South Bank	N 64° 58 25	W 150° 33 12
53	Low Density	Willow	Island	N 64° 58 00	W 150° 35 16
54	Low Density	Willow	Island	N 64° 58 00	W 150° 35 16
55	Low Density	Alder	Island	N 64° 58 00	W 150° 35 16
56	Low Density	Willow	North Bank	N 64° 57 03	W 150° 37 13
57	Low Density	Willow	North Bank	N 64° 57 59	W 150° 37 23
58	Low Density	Alder	North Bank	N 64° 57 59	W 150° 37 23
59	Low Density	Willow	South Bank	N 64° 58 00	W 150° 37 48
60	Low Density	Alder	South Bank	N 64° 58 00	W 150° 37 48
61	Low Density	Willow	South Bank	N 64° 57 12	W 150° 38 55
62	Low Density	Alder	South Bank	N 64° 57 12	W 150° 38 55
63	Low Density	Alder	North Bank	N 64° 57 15	W 150° 39 09
64	Low Density	Willow	South Bank	N 64° 58 19	W 150° 39 55
65	Low Density	Alder	South Bank	N 64° 58 18	W 150° 40 21
66	Low Density	Willow	South Bank	N 64° 58 04	W 150° 41 09
67	Low Density	Alder	South Bank	N 64° 57 50	W 150° 41 39
68	Low Density	Willow	South Bank	N 64° 57 30	W 150° 43 02
69	Low Density	Alder	South Bank	N 64° 57 30	W 150° 43 02
70	Low Density	Willow	Island	N 64° 57 22	W 150° 44 53
71	Low Density	Alder	Island	N 64° 57 22	W 150° 44 53
72	Low Density	Alder	South Bank	N 64° 57 34	W 150° 45 45
73	Low Density	Willow	Island	N 64° 57 42	W 150° 46 08
74	Low Density	Willow	Island	N 64° 58 16	W 150° 47 49

APPENDIX B. COMPARISON OF DIAMETER AT POINT OF BROWSE TO CURRENT ANNUAL GROWTH CHARACTERISTICS OF EACH FORAGE SPECIES

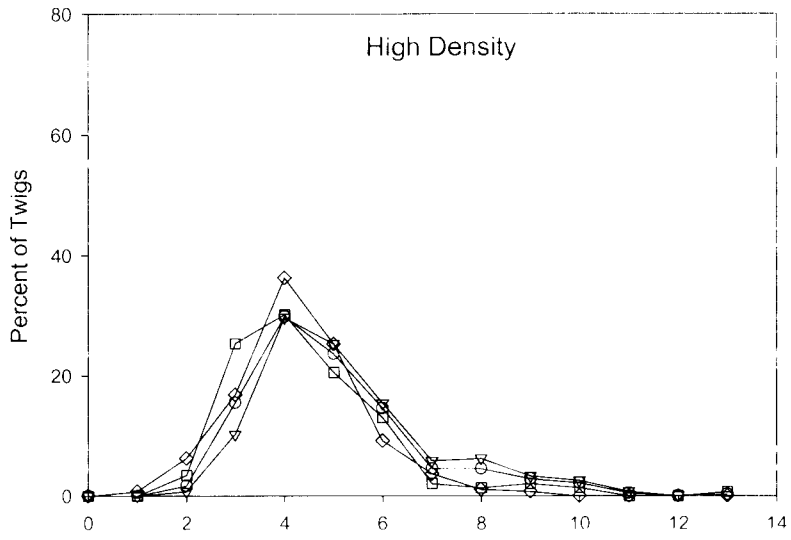
Index

List of Figures

Introduction

The following figures are provided as a comparison of browse selection by herbivores (DPB) within plant species and twig growth characteristics of forage species in willow communities along the Tanana River. These figures illustrate the range of bite sizes (DPB) selected by moose in high and low density areas, as well as the size of twigs browsed in relation to randomly selected twigs. Note the wide variation in DPB and CAG base diameters selected in the high density area.

a)



b)

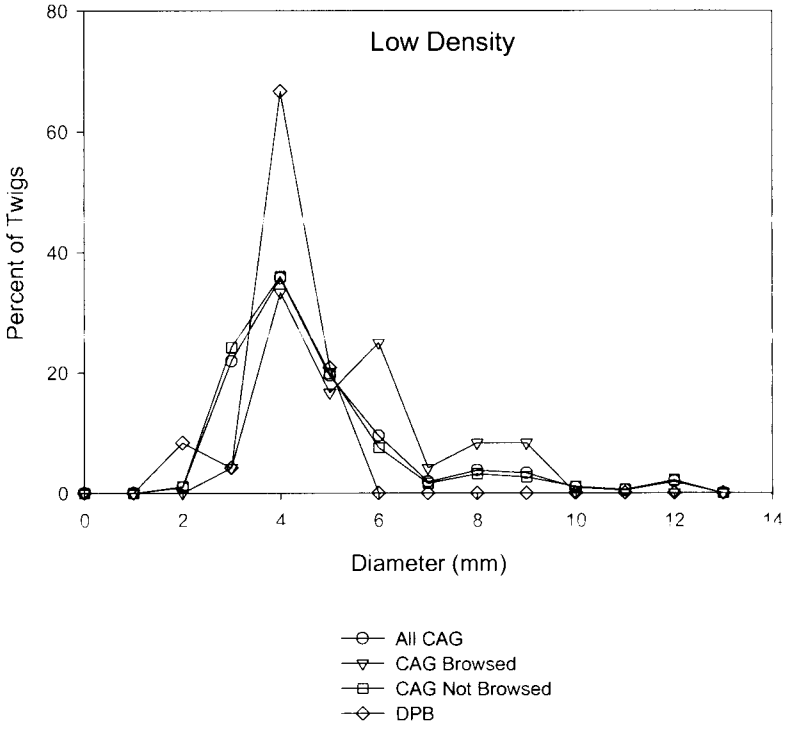


Figure B.1. Frequency distribution of *S. alaxensis* in the high density area (a) and low density area (b) along the Tanana River, Alaska 2001.

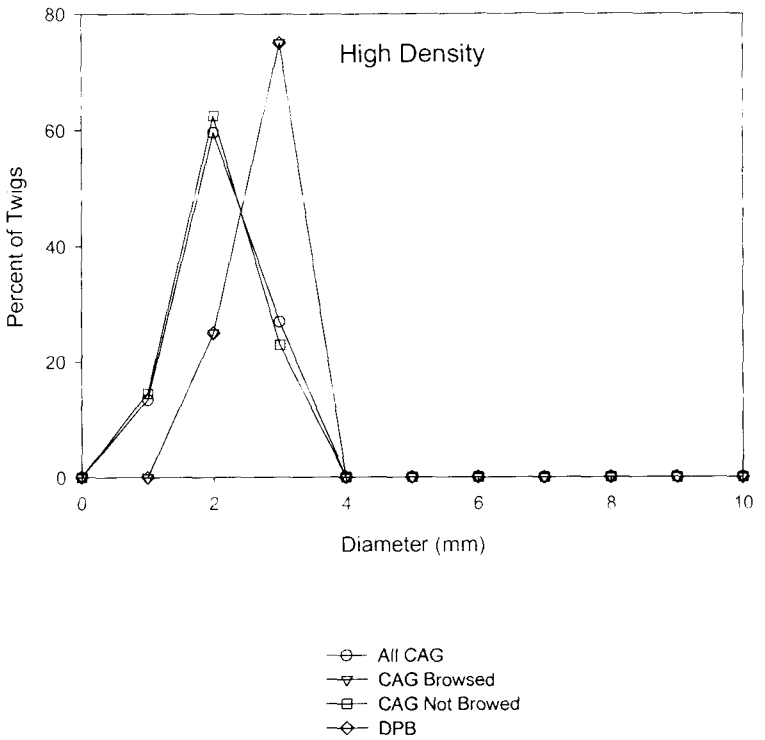
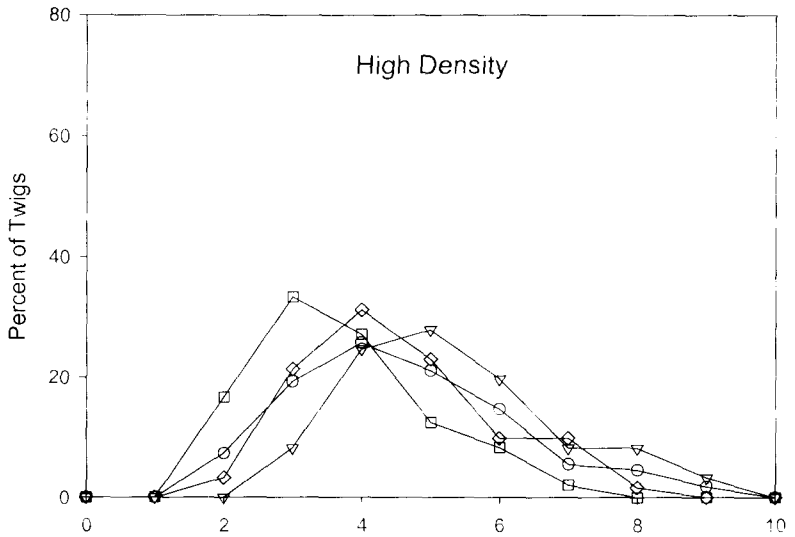


Figure B.2. Frequency distribution of *S. brachycarpa* in the high density area along the Tanana River, Alaska 2001. *S. brachycarpa* was not observed in the low density area.

a)



b)

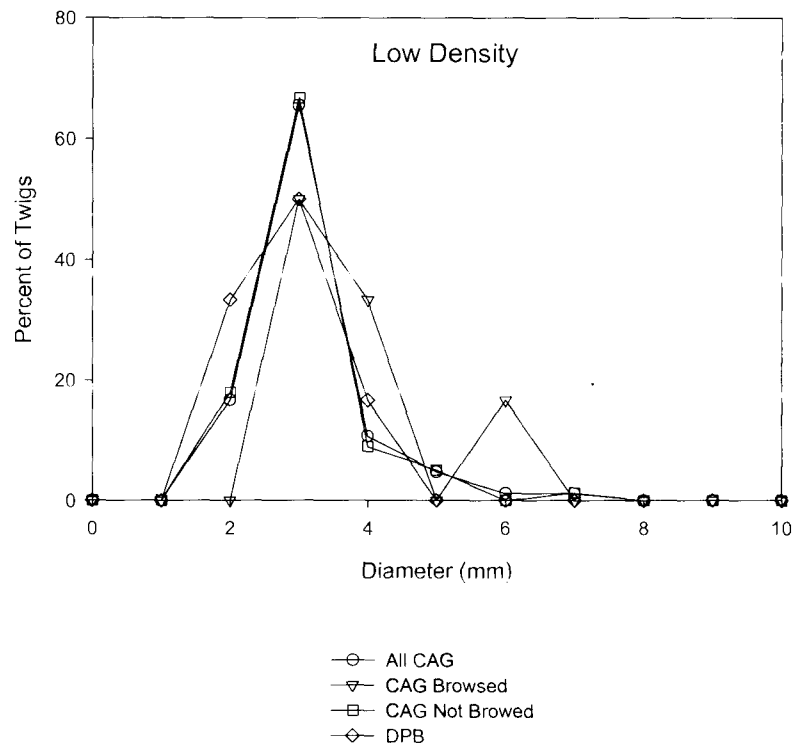
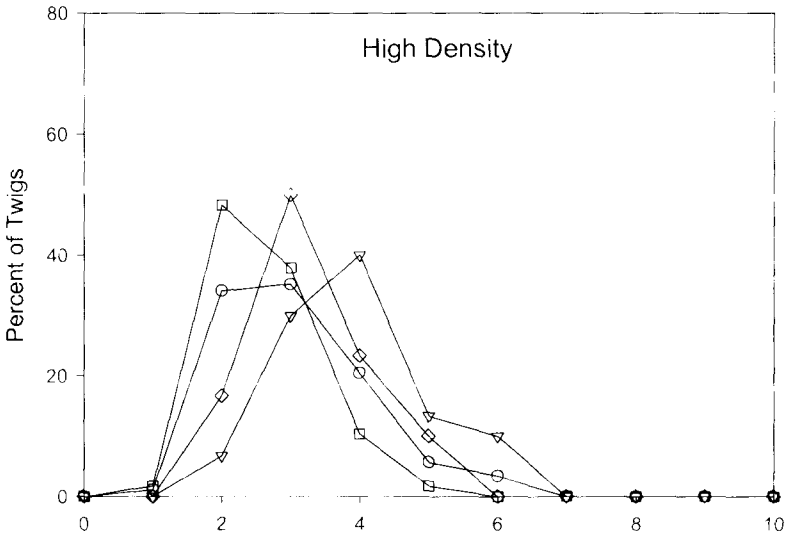


Figure B.3. Frequency distribution of *S. lasiandra* in the high density area (a) and low density area (b) along the Tanana River, Alaska 2001.

a)



b)

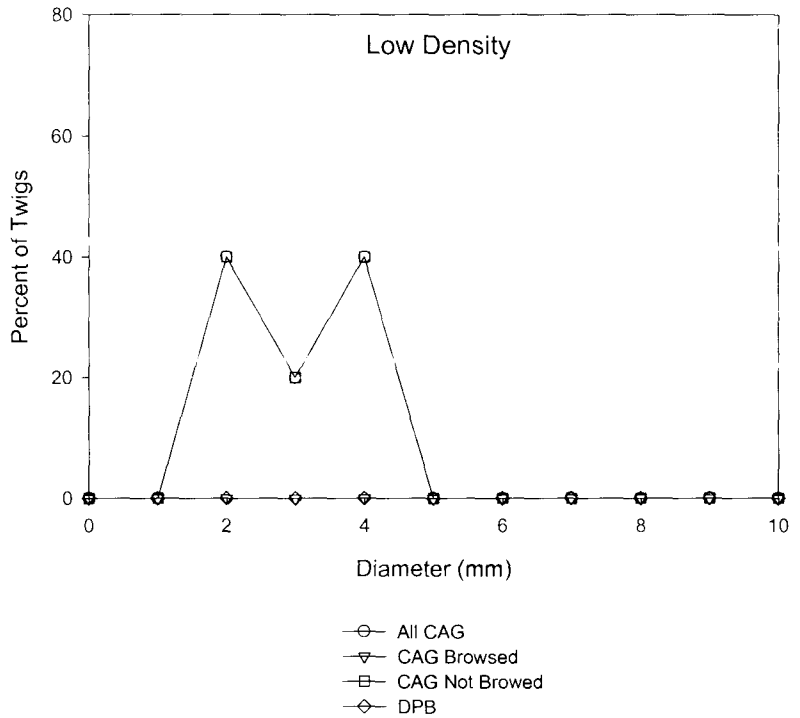
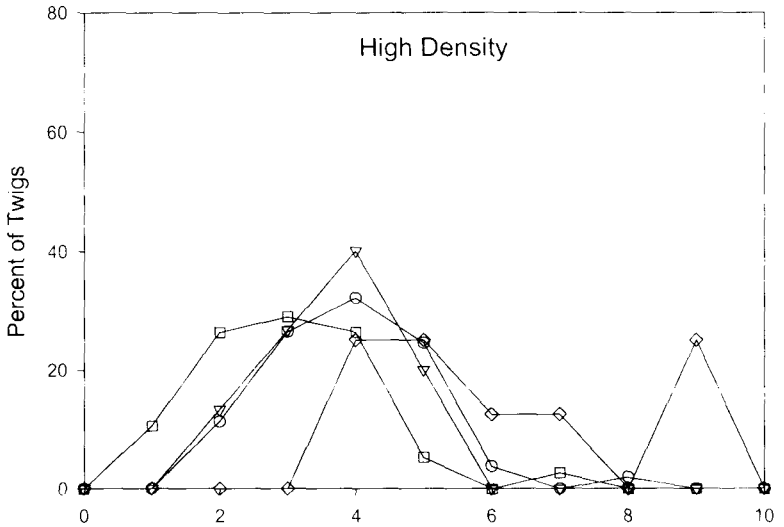


Figure B.4. Frequency distribution of *S. nova-angliae* in the high density area (a) and low density area (b) along the Tanana River, Alaska 2001.

a)



b)

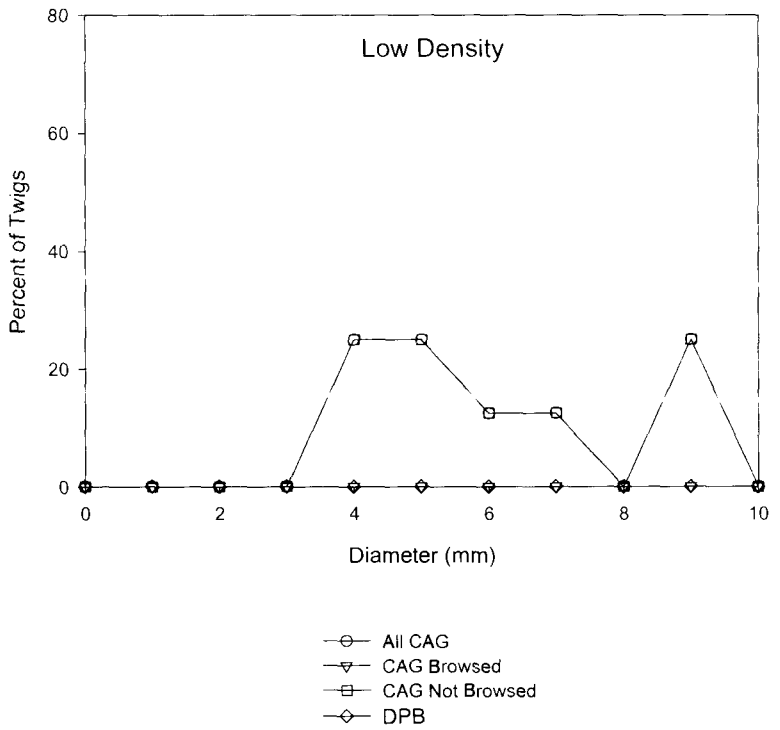


Figure B.5. Frequency distribution of *P. balsamifera* L. in the high density area (a) and low density area (b) along the Tanana River, Alaska 2001.

APPENDIX C. CONCEPTUAL FRAMEWORK OF MODEL

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List of Figures

Introduction

This appendix summarizes the equations and assumptions of each frame type used in the model simulating the effects of erosion, accretion and herbivory. It is included in this thesis to provide a conceptual idea of how the model functioned and the assumptions I made for each model frame.

The landscape of this model represented a 2 km^2 area composed of a grid of 100 x 200 pixels each representing a 10 x 10 m area. All pixels were initially classified as the bare soil frame type. Before the model simulation began, a river was simulated in the landscape grid using the cosine function described in the river frame text below. The simulated landscape functioned according to the following rules. I used a 1 year time interval (Δt) to monitor year to year changes and allowed the landscape simulation to stabilize for 250 years before recording data. Each combination of herbivory, erosion and accretion was replicated 100 times.

Conceptual Framework

River Frame

Assumptions

1. Pixels classified as River can only transitions to bare silt.
2. Accretion of new soils is equal to the probability of erosion.

Equation to Determine River Movements

The model assigned pixels to the river frame in the simulation regardless of their current frame type according to the following equation:

$$A * \cos(W * (x - \Delta t * D)) \pm \frac{W}{2}$$

Parameter	Initial Value	Description
A	800	Amplitude – River bend width (m)
W	2000	Wavelength – Distance between successive river bends (m)
X	-	Column in landscape grid for which river position is calculated
Δt	1	Change in time between river position calculations (yr)
D	0 to 15.1	Erosion/Accretion – Distance river moves in one year (m/yr)
W	60	Width of the River (m)

The framework computes the position of the river for a given column (x). Any pixel within 'Width/2' distance of the river will become river and any pixel beyond that distance will either remain unchanged, or become bare silt if it was river previously. Hence Width actually represents the total river width. This gives the position on the xy plane in meters. This will then be converted to rows by dividing by pixel size, then offset by half the rows in the model.

Bare Soil Frame

Assumptions

1. Pixels classified as bare soil in this model are above mean water level.
2. There are no obstacles to seed dispersal.
3. Bare soil above mean water level is colonized by willow in year 1.

Equation for the Transition to the Willow Frame

Willow initially colonizes bare soil quickly due to its high dispersal through the wind. The density of plants, though relative, is the characteristic used to distinguish young willow communities from bare soil along the Tanana River. Hence, willow density was used to determine when pixels classified as bare soil transition to the willow frame according to the following equation:

$$\frac{dDensity_W}{dt} = W$$

$$Density_{W(t)} = Densiy_{W(t-1)} + \frac{\partial Density_W}{\partial t} * \Delta t * RN$$

Parameters	Initial Value	Description
$\frac{dDensity_W}{dt}$	-	Derivative of willow biomass equation
$Density_{W(t)}$	-	Willow density in the current year of the model (willow/m^2)
W	8	Constant, change in willow density
Δt	1	Time increment (yr)
RN	0 to 1	Random number
$Density_c$	8	Critical willow density (willow/m^2)

Transition Rule:

Transition to Willow Frame when $WillowDensity_t > Density_c$

Willow Frame

Assumptions

1. Willow is the first plant stage of primary succession along the Tanana River.
2. Initial willow biomass is 1 g/m^2
3. Initially poplar and alder biomass is 1 g/m^2
4. Nutrients and seeds are distributed equally throughout the landscape.

Equations for the Transition to the Alder Frame

Transition from the willow frame to the alder frame occurs when the ratio of willow biomass to the biomass of later successional species reaches a critical value (Kielland et al. 1998). In field studies, willow communities along the Tanana River were composed of willow (*Salix spp.*), alder (*Alnus tenuifolia*) and poplar (*Populus balsamifera* L.). The growth of willow plants was effected by the presence of herbivory. The model first calculates the effect of herbivory on willow growth (H_W) and on alder and poplar growth (H_{PA}) in relation to the amount low herbivory area observed in field studies.

$$H_W = \frac{1 - \frac{Percent\,Removed}{100}}{\frac{Percent\,Remaining_L}{100}}$$

$$H_{PA} = \frac{1 - H_W}{a + 1}$$

Parameters	Initial Value	Description
H_W	-	Effect of herbivory on willow growth
PercentRemoved	0 to 80	Percentage of twigs removed by herbivores in model simulation
$PercentRemaining_L$	85	Percentage of forage twigs not removed by herbivores in the low herbivory study area
H_{PA}	-	Effect of herbivory on poplar and alder growth
a	0.6	Constant

The model then calculates the change in willow biomass and poplar and alder biomass per year based on observed growth rates on the landscape. Willow biomass was fit to the logistic growth equation after conversion to the natural logarithmic scale.

$$Ln(AGB_W) = M * (1 - e^{(-k * Age)})$$

where Age is the age of the willow community and M and k are constants. This equation did a reasonable job of explaining variation in the biomass of willow communities based on stand age (R^2 = 0. 88 and 0.92 in the high and low herbivory areas respectively, Figure C.1). The derivative of this equation was used to estimate the amount of new willow biomass in model calculations.

$$\frac{dAGB_W}{dt} = k * M * e^{(-M/(e^{(-k*t)}-1)-k*t+M)}$$

Poplar and alder biomass in observed willow communities exhibited exponential growth and were fit to the equation

$$Ln(AGB_{PA}) = x * Age$$

where age is the age of the willow community observed and x is a constant. This equation fit the observed poplar and alder biomass in field studies (R^2 = 0.93 and 0.77 in the high and low herbivory areas respectively, Figure C.2). The derivative of this equation was used in the model calculations to simulate the growth of poplar and alder during each time step.

$$\frac{dAGB_{PA}}{dt} = x * H_{PA} * e^{(x*H_{PA}*t)}$$

Values used in the model for these equations reflect the values observed in the low herbivory area. The herbivory variables then used to modify the change in biomass to mimic the expected growth under the simulated herbivory level.

Parameters	Initial Value	Description
$\frac{dAGB_W}{dt}$	-	Derivative of the willow biomass equation
$\frac{dAGB_{PA}}{dt}$	-	Derivative of the poplar and alder biomass equation
M	8.55	Logistic equation – maximum willow biomass
k	0.15	Logistic equation – slope of willow biomass
t	-	Stand age
x	0.18	Slope of $biomass_{PA}$ curve

The yearly growth was multiplied by the time interval of the model (Δt), a random number (RN) and added to the biomass currently in the pixel.

$$AGB_{W(t)} = AGB_{W(t-1)} + \frac{\partial AGB_W}{\partial t} * \Delta t * H_W * RN$$

$$AGB_{PA(t)} = AGB_{PA(t-1)} + \frac{\partial AGB_{PA}}{\partial t} * \Delta t * RN$$

Parameters	Initial Value	Description
$AGB_{W(t)}$	-	Willow above ground biomass in the current model year
$AGB_{PA(t)}$	-	Poplar and alder above ground biomass in the current model year
Δt	1	Time increment
RN	0.5 tp 2	Random number between 0.5 and 2 with a mean of 1

The random number was selected from a scale of 0.5 to 2 with a mean of 1 to simulate changes in the growing conditions within a pixel that could result in a 50% reduction of growth in poor years or a doubling of production in good years. Each pixel was then

evaluated based on the ratio of willow to alder and poplar biomass to determine if the pixel should be classified as alder.

Transition Rule:

$$BiomassRatio_t = \frac{AGB_{P\&A(t)}}{AGB_{W(t)}}$$

Transition to Alder Frame if $BiomassRatio_t$ is > $Ratio_c$

Parameters	Initial Value	Description
$BiomassRatio_t$	-	Current ratio of willow to poplar and alder biomass
$Ratio_c$	8	Critical ratio for transition from willow to alder

Alder Frame

Assumptions

1. Willow density decreases during the alder stage and is ignored.
2. Alder biomass/m^2 increases, and then decreases as a function of time.
3. Poplar and spruce are tree species and represent the next stage of succession.
4. The density of tree species dictates the transition to the tree stage.

Equations

Pixels that are classified as alder monitor the density of poplar to determine when to transition into the tree frame. The change in poplar density per year was derived to be P. This value was multiplied by the time step of the model and a random number and then added to the pixels previous poplar density.

$$\frac{dDensity_P}{dt} = P$$

Parameters	Initial Value	Description
$\frac{dAGB_W}{dt}$	-	Change in poplar density per year.
$Density_{P(t)}$	-	Density of poplar in current year
P	0.181	Constant, change in poplar density
Δt	1	Time increment (yr)
RN	0.5 to 2	Random number from 0.5 to 2
$Density_{P(c)}$	2	Critical density of poplar at which transition occurs

$$Density_{P(t)} = Density_{P(t-1)} + \frac{\partial Density_P}{\partial t} * \Delta t * RN$$

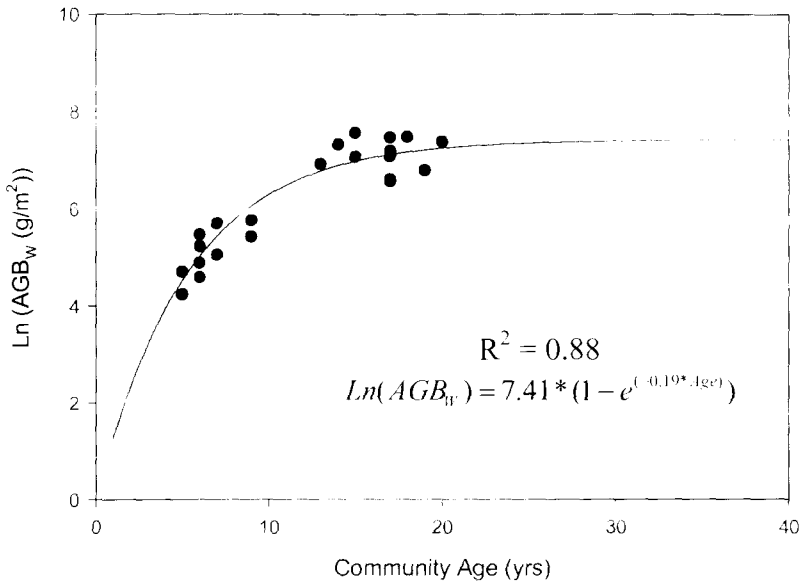
Transition Rule:

Transition to Tree Frame when $Density_{P(t)} > Density_{P(c)}$

Tree Frame

Poplar and spruce stages were not of interest in this model since they represent the end point of primary succession along the Tanana River, so I did not calculate transition parameters for this successional stage. Once a pixel was classified as tree, the pixel retained this value until it was incorporated into the river according to transition rules described in the river frame section. As a result, residence time values reported by the model for the tree frame were not considered usable data since the values varied more with number of years simulated then with the herbivory and erosion/accretion rates simulated in modeling exercises.

a)



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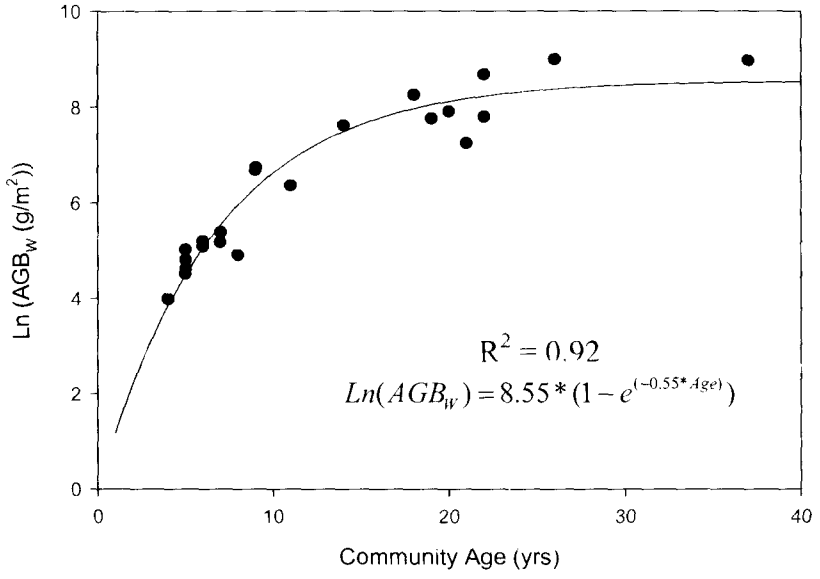
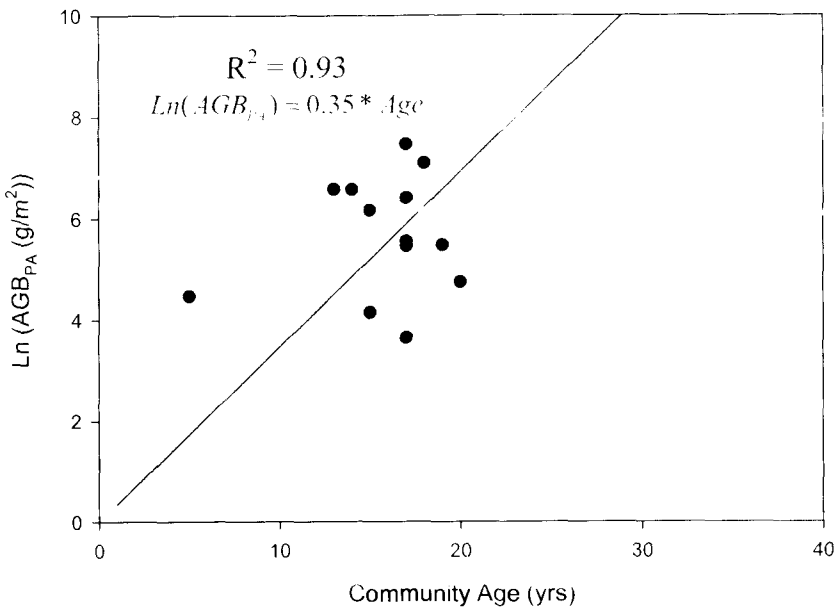


Figure C.1. Relationship between willow biomass and the age of willow communities along the Tanana River in the high (a) and low (b) herbivory areas.

a)



b)

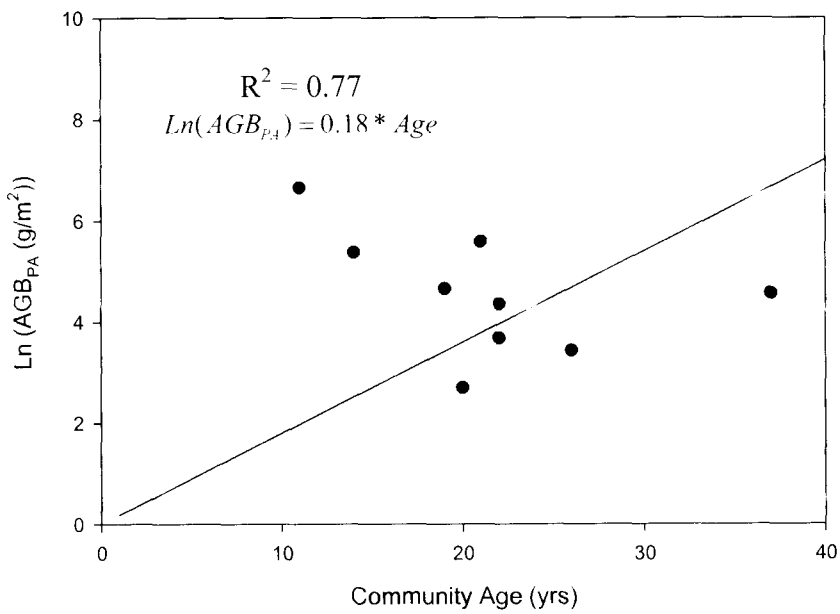


Figure C.2. Relationship between the combined biomass of poplar and alder and the age of willow communities along the Tanana River in the high (a) and low (b) herbivory areas. Fitted line was forced through the origin to simulate plots with no poplar or alder in newly formed communities.